H Virtue Tebbs

With the writer's kindest regard.

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ON THE COMPOUND VISION AND THE MORPHOLOGY OF THE EYE IN INSECTS.

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XIV. *On the Compound Vision and the Morphology of the Eye in Insects. By*

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(Plates XL.–XLIII.)

Read 7th February, 1884.

The manner in which the compound eye of arthropods subserves the function of vision has been an undetermined problem since Johannes Müller enunciated his well-known theory of mosaic vision in 1826 *.

The views of naturalists on this subject, if we except the extremely improbable and purely hypothetical view recently propounded by Exner †, may be grouped under two heads :—some have supported Müller's hypothesis, or a modification of it ‡; whilst others have followed R. Wagner, and held the view more commonly attributed to Gottsche §.

It is well known that Müller supposed that each facet produces a single visual impression and that the whole visual field consists of a mosaic of such impressions; many of his followers have modified this view, by supposing that a small number of visual impressions are originated by each facet, the order of which is neither reversed nor inverted by the dioptric apparatus.

Müller's hypothesis was suggested to its learned author by the radial arrangement of the parts of the compound eye about a hemispherical or nearly hemispherical retina, and by the difficulty of conceiving a retina capable of correcting a mosaic of reversed and inverted images, the order of which is neither reversed nor inverted.

R. Wagner || was the first to throw doubt upon Müller's view: he mistook the capsule of the crystalline cone for a retina, an error which was also committed by Ruete ¶ and Dor **.

R. Wagner and his followers regard the compound eye as an aggregation of simple eyes, the dioptric structures of each producing an image on a distinct retina, in the same manner as the dioptric structures of the vertebrate eye, so that the whole visual field is a *mosaic of reversed and inverted images, the order of which is neither reversed nor inverted.*

The most important paper on this subject, after Müller's work, was undoubtedly a short but well-known contribution to Müller's Archives by Gottsche in 1852. Leeuwen-

* J. Müller, 'Zur vergleichenden Physiol. des Gesichtssinnes des Menschen und der Thiere' &c.

† Sigm. Exner. Biologisches Centralblatt, Jahrg. i. p. 272, and Pop. Science Review, 1881, p. 337.

‡ Helmholtz, Du Bois Reymond, J. Notthaft, &c.

§ Will. Zenker, &c.

|| Wiegmann's Archiv, 1835. Bd. i. p. 372.

¶ Gratulationsschrift der med. Fac. zu Leipzig zu C. G. Carus 50-jähr. 1861.

** Archiv d. Sciences Phys. et Natur. 1861.

hoek had long before observed the images produced by the individual facets. Gottsche observed and drew attention to these: he, I believe, was the first who investigated the structure of the great rods (*Sehstäbchen*), and suggested that the highly refractive axial threads, which he discovered in their interior, in some way transmit the images formed by the lenses to recipient nervous structures beneath.

I can hardly imagine that the earlier writers intended to convey the idea that an image could be transmitted, as Dr. Grenacher facetiously suggests *, "as a message is transmitted by a telegraph wire," but suspect that they meant that rays of light from certain definite points in the image are so transmitted. There is, however, considerable ambiguity about Gottsche's paper on this and other points, although he apparently correctly indicated the position of the true recipient layer, beneath the great rods, without actually observing it.

Gottsche's paper appears to have been completely misunderstood by all his critics, who seem to have imported into it a false analogy between the image in the compound eye, and that in the vertebrate eye: the image is thus supposed to fall upon the retina. If Gottsche had intended to convey such an idea his view would have been, as it is generally supposed to be, in direct antagonism to Müller's hypothesis; yet Müller gave a kind of adherence to Gottsche's view, holding it to be consistent with and supplemental to his own.

It appears to me that the whole tenor of Gottsche's paper is an attempt to modify, not to destroy, Müller's theory, although both he and Müller, in the note which accompanies this paper, seem to have forgotten the difficulty which arises from the inversion of the subcorneal image. And further, Gottsche's retina is not the retina of Wagner, Ruete, and Dor. Soon after the publication of this paper Leydig † drew attention to the continuity of the axial structures of the great rods and the crystalline cones; and supposed the cones to be the terminal organs of the optic nerves. His views on the connexion of the cones and the nerve-centre are not easy to comprehend, as he appears to deny the truth of Müller's hypothesis, at the same time that his observations apparently support it.

Claparède ‡ then pointed out the apparent continuity of the cone and the corneal facet, in *Typhis*, and found that the cornea, cone, and axis of the great rod, in some insects, consist of the same material; he asks, if it is not possible that these are all concerned in transmitting the image to nervous structures beneath them.

In criticizing the views of Gottsche, Claparède, and Leydig, it appears to me that it should constantly be borne in mind, that they worked at a time when the close relation between physical and vital phenomena was less completely understood than at present, and that they consequently, perhaps unconsciously, ascribed hypothetical vital properties to structures, which will not bear rigorous investigation.

Max Schultze § first investigated the optical relations of the great rods, and concluded that they are not the terminal organs of the optic nerve, after a most laborious examination of their structure. He also rejected Müller's hypothesis as optically untenable.

* Untersuchungen über das Sehorgan der Arthropoden, p. 10. Göttingen, 1879.

† Müller's Archiv, 1855, p. 406.

‡ Zeitschrift für wissensch. Zool. Bd. x.

§ Schultze, Archiv, Band ii. p. 404.

Boll and Grenacher have, however, more recently adopted a modification of Müller's hypothesis, based upon a view held by Max Schultze. Gottsche described the very remarkable structures, at the inner extremity of the great rods of the lobster, under the term "*doppel-Pyramiden*"*, better known as the spindles. Max Schultze regarded the spindle as the true nerve terminal; it is the "*Retinula*" of Dr. Grenacher †.

On the other hand Wagner's theory has had numerous supporters, for the weak point in Müller's hypothesis is met by it, as many insects with very few corneal facets have evidently extremely acute vision. The absence of any retina in the position of the image below the cornea is, however, fatal to it.

Another difficulty militates strongly against this theory, which has been already dwelt upon by Dr. Grenacher: the extreme minuteness of the subcorneal image would necessitate recipient retinal elements far smaller than any known to exist in the animal kingdom. Moreover, as each corneal image corresponds, as a rule, to an angle of about fifteen degrees, and as the mean difference in the axes of adjacent facets is not usually half a degree, the images of adjacent facets are nearly identical ‡, a fact in itself almost fatal to Wagner's hypothesis.

Formerly I accepted a modification of Müller's hypothesis §; but a further investigation has led me to discard both the theories of arthropod vision, and to substitute one which is, I believe, in complete accord with all the facts, and which, so far as I know, has not been even suggested by any previous observer.

The compound eye is divided into two parts by a membrane which I shall speak of as the *membrana basilaris*. The structures between this membrane and the cornea are the crystalline cones and the great rods ‖; I regard all these as dioptric structures, and shall speak of the cornea, and all the parts which intervene between it and the membrana basilaris, as the *Dioptron*. I shall use the term *great rod* provisionally to designate the complex structure between each cone and the membrana basilaris, and *segment of the dioptron* for the parts, collectively, beneath each corneal lens.

Beneath the membrana basilaris I have discovered a layer of bacilla, comparable in most respects with the rod and cone layer of the vertebrate, in the place where Gottsche suggested such a structure might exist. This layer is succeeded by others, similar to the nuclear and molecular layers of the vertebrate eye. I shall speak of all these structures as the *Neuron*.

The existence of a continuous basilar membrane, in some arthropods at least, excludes the great rods from any share in the nervous mechanism, a conclusion which also follows from a more complete knowledge of their structure.

Nearly two years ago I made an examination of the eye of a Plume Moth (*Pterophorus pentadactylus*), in normal saline solution, immediately after the death of the insect. I was surprised to find a very considerable deviation from any structure previously described by others or observed by myself. Fig. 3 is a representation of the optical section of a portion of the eye: in this condition the great rods presented the

* Müll. Arch. 1852, p. 484. † *L.c.* ‡ Phil. Trans. 1878, pt. ii. pp. 596, 597.
§ Phil. Trans. *ibid.* p. 577. ‖ "Rhabdia" *mihi*, Phil. Trans. *l.c.*

appearance of ovoid spindles, each enclosed in a cylindrical sheath. The spindle-shaped bodies underwent rapid change of form from the escape of their contents, so that in a short time they were reduced to the condition of empty shrivelled tubes.

Further observations on various insects have convinced me that such changes usually occur shortly after death, either from osmosis or from alterations of tension.

These observations suggested to me the possibility that the spindles of the great rods should be regarded as lenses of very short focal length, but of great thickness, and that they form a second refractive system, the anterior foci of which correspond with the subcorneal images, and the posterior foci with the bacillar layer of the retina.

According to this view the dioptron is composed of an anterior and a posterior refractive system.

The anterior refractive system of each segment of the dioptron consists of a corneal facet, a lenticulus, to be hereafter described, and the anterior face of the crystalline cone.

These parts form a *subcorneal image*, which lies in the anterior focus of the posterior refractive system.

The posterior refractive system magnifies the subcorneal image, and erects it, at its posterior focal plane, upon the bacilla of the neuron.

It is well known that if an objective is placed in the reversed position beneath the stage of a microscope, and the instrument is focussed for its posterior focal plane, it can be used as a telescope. A segment of the dioptron of an arthropod's eye, according to my view, is comparable to such an instrument, and the whole dioptron to as many instruments as there are segments, each giving a perfect picture of the objects which subtend a small angle with its axis; and thus a mosaic of images, which are erect and not reversed, falls upon the retina.

Although the ordinary simple eyes of insects do not exhibit any structure comparable to the second refractive system of the dioptron, the simple eyes of many larval insects have a posterior refractive system, and afford a complete transition from a simple to a compound eye.

I shall now proceed to the consideration of the details of structure and measurement on which my theory is based, in the following order:—

I. The Anatomy and Functions of the Dioptron.
II. The Anatomy and Functions of the Neuron.
III. The Development of the Compound Eye.
IV. The Morphology of the Eyes of Arthropods.

I. The Anatomy and Functions of the Dioptron.

The dioptron in the most highly specialized forms of compound eye, such as are found in the majority of perfect insects, is entirely enclosed in a chitinous case, formed by the compound cornea and the basilar membrane, united to each other by an inflection of the integument, which forms a short hollow cone between them.

The cornea and the basilar membrane are nearly parallel surfaces, so that the whole

dioptron has the form of a round or oval truncated cone, of which the base and apex are subspheroidal or, more generally, cycloidal surfaces *. The older writers named the inflected ring which unites the cornea and the basilar membrane "*the sclerotic*"; I shall designate it the *scleral ring*.

The inner margin of the scleral ring is often thickened, and receives the insertion of one or more muscles (figs. 1 & 1*a. mc.*), which are probably concerned in the adjustment (accommodation ?) of the optical apparatus.

The whole interior of the dioptron is divided more or less perfectly into hexagonal or square tubes by fine sheaths † which extend from the margins of the corneal facets to the basilar membrane; each encloses a cone and a great rod, and forms a segment of the dioptron.

The great eyes of the dragon flies (*Æshnia* and *Agrion*) have enabled me to detect large lymph-sinuses (*a.b.* figs. 5 & 9) which pass through the scleral ring and connect the lymph-spaces of the dioptron with those of the head.

In *Æshnia* the afferent vessel (*a*) enters the superior internal border of the dioptron: it has distinct walls, and is the anterior extremity of the bifurcated aorta ‡. I am unable to say that this is general in insects, but from what I have seen I suspect that it is.

The efferent openings (*b.b.* figs. 5 & 6) are situated in the lower portion of the scleral ring, nearly opposite to the afferent vessel: they are generally, even in very different insects, long slits, across which a number of radiating nucleated fibres *rf* are stretched, between the basilar membrane and the scleral ring. These in sections, vertical to the basilar membrane, present a fan-like arrangement similar to that of the ciliary muscle of the vertebrate.

I have been unable to make out any striæ in these fibres; and as non-striated muscles are not known to occur in insects, I hesitate to regard them as contractile, although one is almost tempted to such a belief from their arrangement and position; perhaps they are simply elastic bands which maintain the tension of basilar membrane, where its attachment to the scleral ring is defective, to permit the circulating fluid to pass out of the dioptron. Their occurrence, however, in the simple eye (fig. 33, *ls.*) around the edge of the corresponding membrane is indicative of an active function.

The tracheal vessels (*t.v.*) of the dioptron consist of a main trunk, which almost surrounds the edge of the basilar membrane, from which numerous branches ramify and anastomose on the neural surface of the membrane (fig. 68).

Vessels from this network perforate the basilar membrane and run outwards, almost to the cornea, between the cuticular sheaths of the segments of the dioptron; they terminate in blind extremities.

In the *Syrphidæ* the tracheæ of the dioptron assume the form of fusiform sacs between its segments; these have very narrow necks where they pass through the basilar membrane.

The basilar membrane is a cuticular structure, which was described by Leydig as a

* Phil. Trans. *l.c.* p. 595. † "Umhüllungsschläuche" of Leydig & authors.

‡ 'Anatomy of the Blowfly,' by the author, plate ix. fig. 1.

fenestrated membrane *, and it is usually believed to be perforated for the passage of nerve-fibres to the great rods. In many sections it is easy to see that the membrane is continuous, except where it is perforated by the tracheal vessels. In the great Dragon-flies it is also undoubtedly pierced by the fringes from the pigment-cells of the dioptron, which intercommunicate with the fringes of the pigment-cells, situated on the neural surface of the membrane (fig. 69). In some insects the membrane is actually thickened at the inner terminations of the great rods, so as to form small lenticular swellings (fig. 71); and in a specimen of the eye of a lobster, in which the neural elements beneath the great rods are not in the same line with them, the swellings are prismatic (fig. 70).

In some insects, especially in *Notonecta*, the basilar membrane is strongly ridged, the ridges corresponding with the attachment of the cuticular sheaths of the segments of the dioptron. It is apparently defective in parts, the openings being closed by the cellular layers which cover the two surfaces of the cuticular membrane.

In the crane flies † (*Tipula*), in some Coleoptera (*Telephorus*), and in other insects in which the component segments of the dioptron resemble distinct ocelli rather than parts of a compound eye, the cuticular sheaths of the great rods extend inwards, and also include the nervous structures. The basilar membrane then appears to be actually perforated, so that the inner extremities of the great rods come into contact with the nerve-terminals. This condition, however, is very exceptionnl, and is capable of explanation from the manner in which the parts are developed.

I shall recur to the consideration of the question of the passage of nerve-fibres through the membrane when I discuss the function of the great rods and the bacilla of the neuron ‡.

The various modifications of the cornea will be more conveniently considered hereafter; I shall only mention in this place the fact that in all those cases in which there are no lenticular facets, and where the cornea is simple and continuous, the outer face of the crystalline cone is strongly curved, being a portion of a prolate spheroid, and therefore probably capable of producing an image of great sharpness. Such a surface has, as is well known, the property of forming a perfect image, when the eccentricity of the generating ellipse is the reciprocal of the refractive index, a condition which appears to me to be very nearly attained in the curvature of these cones.

Prolonged investigation has gradually convinced me that the very considerable differences which the plan of the arthropod eye exhibits in different species and families are due to differences in the consistency and chemical nature of the parts. The highly refractive structures may consist of some modification of chitin, or some allied albuminoid, or of an oil-like fluid contained in the meshes of a fine stroma and enclosed in elastic capsules.

In the former case, where the refractive medium is chitinous, it undergoes but little change of form in the preparation of microscopic sections: in the latter case the fluid escapes from its capsule, and the whole appearance of the parts is modified, even when such solvents as clove oil and absolute alcohol have not been used; and the appearances are still further altered by the use of such fluids in the preparation of sections.

* Müller's Arch. *l.c.* † Phil. Trans. 1878, *l.c.* p. 579. ‡ See page 409.

In most insects a lens lies under each corneal facet; I shall show hereafter that this lens is sometimes formed from the outer portion of the crystalline cone, and in other cases from the cornea itself, which then assumes the appearance of a honeycomb, the cells containing the lenses.

The consistence of the lens seems to vary very much; in some cases it is apparently fluid, enclosed in an elastic capsule; in the Earwig and the Cockroach I have even been able to separate such lenses from the cornea by pencilling its inner surface; the capsules can then be ruptured, and the fluid seen to escape by pressing on the cover glass; the ruptured capsules exhibit a single tear and fine wrinkles (fig. 21) *.

The refractive index of the fluid with which the lenses are filled is very nearly 2·0; this fluid appears like an oil, but it undergoes slow solution and decomposition by the action of water and weak saline fluids; a comparatively lowly refracting fluid and a fine reddish molecular substance result from their action.

The oil-like fluid is rapidly dissolved by ether and is blackened by osmic acid. Only the red molecular precipitate remains in specimens prepared in the usual way with clove oil. I believe the great brilliancy of the cornea of many insects during life is due to this fluid lens immediately beneath its surface, and that the loss of brilliancy which occurs soon after death, is due to the decomposition of the fluid, or its escape from the lens-capsule.

I am inclined to regard this fluid as an oil of complex constitution, which is possibly rich in sulphur or phosphorus, to which it owes its high refractive index and ready decomposition. Observations with a micro-spectroscope have given negative results.

In other cases the lens, when separated, breaks up like a viscid body; the lens-capsule always appears to contain a stroma, the meshes of which the fluid permeates; and the consistence of the lens depends on the relative amount of the stroma.

Every one who has examined the compound eye since improved methods have been adopted, must have been puzzled by the "*nuclei of Semper*" which figure so prominently in the descriptions of Claparède †. I formerly supposed with Dr. Grenacher that Claparède so designated the nuclei which are frequently seen in the immature eye between the crystalline cone and the facet of the cornea (*cn.* fig. 3). But such a view is by no means satisfactory.

I was very much surprised on one occasion, to see the "nuclei of Semper," which are really nothing but the shrivelled segments of the lens-stroma, appear suddenly in a compound cornea treated with ether on the stage of the microscope; as the oil dissolved out of the lenses the contents of the capsules split into four parts. I regard this as the result of the shrinking of the stroma. A similar appearance is seen when the cornea of an insect is examined after having been allowed to become partially dried. I have never observed this in specimens prepared in the usual manner with alcohol and clove oil.

In the simple eyes of caterpillars, "*ocelli compositi*" (figs. 36–40), which are un-

* This lens was described by Müller; but its existence has been completely overlooked by recent authors.

† Zeitschr. f. w. Zool. Bd. x.

doubtedly nearly related to the compound eye, a subcorneal lens exists. In these it consists of three segments. A similar lens is seen in the semicompound eyes of isopods, and is regarded by Dr. Grenacher as a cone in a highly modified condition. It consists of only two segments instead of three or four.

The cornea and oil-lens together have a very short focus. The picture formed by these structures is usually from five to ten micromillimetres behind the posterior surface of the lens.

Very great differences of opinion have obtained credence concerning this image since the publication of Gottsche's paper. Many authors, and quite recently Exner *, have denied that any images are formed by the eye when the crystalline cones are *in situ*. I have a specimen of the cornea and cones of a moth (*Smerinthus populi*), mounted in balsam, in which distinct images are formed in the interior of the crystalline cones. In Exner's experiment the crystalline cones were surrounded by a lowly refracting fluid. As the images, according to my calculations, are formed near the focal plane of the inner ends of the crystalline cones, rays emerge from the inner extremities of the cones as parallel rays, or at least approximately parallel. The image cannot therefore be observed by the high powers of a microscope. Exner is undoubtedly quite right when he says that no image can be observed when the cones are *in situ* and surrounded by a lowly refractive fluid; but it by no means follows that none is formed. Indeed the structure of the eye is such that an image must be formed, and it cannot be neglected in working out the manner in which the eye acts as an organ of vision.

The focal length of the corneal lenses of the Fly (*Musca vomitoria*) has been given by me from actual measurement as $\frac{1}{400}$ of an inch †. I have since found that the results obtained by measurement are always greater than those arrived at by calculation; this is partly due to the rapid loss of refractive power immediately after death, but also to the fact that any moisture adhering to the inner aspect of the lenses forms a concave surface as it is attracted by the inflected margins of the corneal facets. I believe that the only satisfactory results are those arrived at by calculation. The greatest difficulty is the estimation of the refractive index. This is often considerably greater than that of Canada balsam, which is sufficiently proved by the formation of a subcorneal image when the cornea and cones of a moth are entirely immersed in it.

Small fragments of glass in water have nearly the same brightness as the cones and lenses of a moth in balsam. By reducing the illumination of the field of the microscope both were just visible with the same illumination, which indicates a refractive index, for the cones and lenses, of 1·8 nearly. Assuming the refractive index to be between 1·5 and 2·0, the focus by the formula $\left(\frac{1}{\mu-1}\right)\frac{rr'}{r+r'}=f$ will lie between r and $\frac{r}{2}$, when $r=r'$. the value of the fraction $\frac{r\,r'}{r+r'}$ varies between 10^{μ} and 20^{μ} in different insects which I have examined. Therefore the focal length of the corneal lens is from five to twenty micromillimetres, and falls well within the crystalline cone, and the rays frequently emerge

* Biol. Centralblatt, i. p. 280.

† Phil. Trans. *l.c.* p. 585.

from the posterior end of the cone as approximately parallel, a conclusion which I arrived at formerly *.

In a specimen of the cornea and cones of the moth (*Smerinthus populi*) mounted in balsam, the micrometer screw shows the distance of the image behind the posterior surface of the corneal lens to be about forty micromillimetres, estimating the refractive index of the lens at 1·68 and that of the balsam at 1·5 $\therefore \frac{1 \cdot 68}{1 \cdot 5} = 1 \cdot 12$, and $40 : \frac{1}{1 \cdot 12} :: f : \frac{1}{1 \cdot 68} \therefore f = 26$ micromillimetres approximately. The radius of curvature of the anterior surface of the corneal lens is about forty micromillimetres, and the distance between its anterior and posterior surfaces is 10 micromillimetres, which would give a focal distance of 26 micromillimetres measured from the posterior surface as before, with the same refractive index.

The diameter of the image is approximately 20 micromillimetres, in the same balsam-mounted specimen; it corresponds to an angular aperture of 24 degrees. The distance is $10 \times \cot 12° = 47$ in micromillimetres behind the optic centre; which does not differ widely from the above. The angle was determined by using two lighted tapers as the object. The error arises from the difficulty of determining the exact size of the image, that is the distance between the focal points. Of course the plane mirror of the microscope was used in making these measurements.

I formerly † gave the approximate length of the focus of the corneal facets of the hornet as $\frac{1}{200}$ of an inch; it is easy to see that it should have been $\frac{1}{2000}$, with a refractive index which I estimated at 1·53, which is too low, as the refractive index is nearly 2·0 during life—a result which is sufficiently near those given above.

If we assume the outer ends of the great rods to have a spheroid curvature convex towards the cone, the posterior focus of which corresponds to the bacillar layer, all the mechanism is present for the formation of an erect magnified image of the central portion of the subcorneal inverted image upon the sentient structures.

In many insects I have observed such a conformation of the outer ends of the great rods as this theory requires, and I believe that when observation fails to show such an arrangement, this is due to the very profound modifications which these structures undergo when removed from the eye, or during the preparation of the eye for investigation.

J. Müller regarded the great rods as nerve-terminals, a conclusion which was justified by his want of knowledge of their structure, but which is no longer tenable. Gottsche first discovered the compound nature of the great rods, and described, as I have already mentioned, the inner extremities of those of the lobster, as "*double pyramids.*" The structure to which he gave this name is now better known as the spindle; Dr. Grenacher speaks of it as a "*Retinula.*"

Max Schultze examined the structure of the great rods and their spindles in the lobster; he came to the conclusion that the rods are not the receptive elements, but ascribed this function to the spindles. Max Schultze founded this opinion chiefly on

* Phil. Trans. *l. c.* p. 581.

† Phil. Trans. *l. c.* p. 581.

two characters which he had observed in these structures—their tendency to split into transverse disks and their pink colour in the lobster.

The structure and development of the spindles varies considerably in different Arthropods. Sometimes they occupy the whole interior of the great rods, extending from the basilar membrane to the apex of the cone, as in the flies, and more obviously in the eye of the Water Boatman (*Notonecta*); in a greater number of insects, however, they are separated from the cones by a considerable space, the interval being occupied by an albuminous fluid or semifluid substance enclosed in a cuticular sheath, which is surrounded by pigment-cells (fig. 22. *ch.*).

The albuminous contents of this cuticular sheath have a low refractive index, and partially enclose both the cone and the spindle. The diameter of the tube which intervenes between the cone and spindle is subject to considerable variation in the same species of insect. In moths it is usually a very fine thread in specimens prepared by section; but in the recent eye of the very species in which it appears in this form in sections, I have frequently found the tube as wide as the base of the cone (figs. 3 & 27). I believe that the contracted condition is produced by the escape of its contents and the great elasticity of the cuticular sheath itself.

In the perfectly fresh eye of an insect the spindles are very transparent ovoid bodies, attached by their bases, which are truncated, to the membrana basilaris, and surrounded by pigmented fringes from cells, which cover the outer surface of the basilar membrane between the spindles (figs. 2, 3, & 10. *sp.*).

The appearances which the spindles assume after death and in sections prepared for microscopic examination are very various. In the noctuid moths they then appear as chitinous rods; sometimes they even present a stellate transverse section. In a specimen of the eye of a moth (*Hemerophila perfumaria*), prepared with osmic acid and afterwards mounted in balsam, they have assumed the form of absolutely empty shells, which are blackened intensely by the acid.

The spindles of a yellow Underwing (*Triphæna pronuba*, fig. 22 *sp.*) from a specimen preserved in a solution of chloral hydrate which was not replaced by any other fluid, resemble tubes filled with minute spherical granules, which give them a transversely striated appearance. These spindles are white and opaque when seen with reflected light.

In all these cases the form and appearance of the spindle are very different from that which it presents in its normal unaltered condition. The outer end always contracts much more than the inner, so that it has a strong tendency to assume the form of a wine-bottle with a long neck. In the Crane-flies (*Tipula*) I have found that the length of the narrow part of the spindle varies greatly in different specimens (figs. 10–13), so that there is no difficulty in connecting the normal ovoid spindle with the bottle-shaped organ which is usually seen in microscopic preparations.

The spindles of the Crane-flies (*Tipula*) are seen, in transverse sections, to be composed of seven tubes (fig. 14).

In some recent preparations I have succeeded in isolating these (fig. 13); they then curl and twist in a very remarkable manner, in water and glycerine, and they are easily

ruptured by pressure on the cover-glass, when a highly refractive oil-like fluid escapes from them. The axial structure of the great rods in other insects (*Notonecta*) exhibits the same appearances, some of which are figured by Dr. Grenacher*, and I have no doubt that the very fine axial threads seen in the great rods of flies are the shrivelled remains of the spindle.

In the true flies (Muscidæ) the great rods are very highly modified; each consists of six cells (sheathing-cells); these enclose the axial spindle. This can only be satisfactorily examined, in the recent eye, by very careful teasing. The great rods may be thus separated either in normal saline solution, or in very dilute osmic-acid solution, ·05 per cent.; in the former fluid the sheathing-cells undergo very rapid disintegration by vacuolation, but this occurs less rapidly in the osmic solution.

The sheathing-cells surround a structure which is fluted like a column, the "Rhabdom" of Dr. Grenacher. This is the spindle; it consists of an elastic sheath, apparently composed of from four to seven component tubes filled with a highly refractive fluid. The fluid rapidly escapes from the injured tubes in minute glistening drops, whilst the tubes themselves become converted into fine threads. In the recent condition the slightest pressure suffices to empty the spindles. The various appearances of the component tubes are represented in the figures (figs. 16–18).

The tubes of which the spindle is formed apparently intercommunicate at the inner portion of the spindle. They twist and curl in glycerine and water as well as in normal saline solution. They are very elastic, and are easily drawn out to several times their proper length, which they regain when the tension is relaxed.

The fluid contents of the spindle are soluble in ether and clove-oil. The fluid is perfectly colourless in the Blow-fly; but the same fluid in the cabbage butterfly has a bright ruby tint when seen through the length of the spindle.

In ordinary transverse sections (fig. 20) the spindle is seen to contain a cavity surrounded by a plicated wall. The boundary of the irregular lumen exhibits six or seven, more rarely four, bright spots: these are the sections of the threads. All these details are correctly figured by Dr. Grenacher †. The outer extremity of the spindle in the flies is nearly hemispherical, and is imbedded in a structure which I formerly described as a tetrasome. This structure, in preparations hardened in chromic acid and its salts, has the appearance of four small spheroid bodies; but in some remarkably distinct sections which were fixed with osmic acid these are seen to be the four segments of a minute lens. The form and relation of this structure to the spindle will be best understood by a reference to fig. 19.

In the Lepidoptera the distance of the external end of the spindle from the cone appears to depend on the habit of the insect. It is furthest removed in the Noctuids, and closest in the Diurna: that is, in the Noctuids it is a larger lens of longer focal length, and therefore it receives a much larger cone of light-rays; in the Diurna the body which I formerly named the "*tetraphore*" ‡ appears to be the external portion of the posterior refractive system.

In the Hymenoptera and Neuroptera, it is very difficult to see the parts in their normal

* *L. c.* figs. 51–53.

† *L. c.* fig. 62.

‡ Phil. Trans. *l. c.*

condition, as the walls of the refractive structures are very thin, so that in all the specimens which I have examined, the tubes of the spindle, which is very similar to that in the flies, had collapsed.

There are usually two principal layers of pigment in the dioptron—an outer layer, which is thickest at the apices of the cones (fig. 1. pg^1), and an inner layer (pg^3) at the inner extremities of the spindles.

The pigment of the outer layer is generally contained in cells which form a kind of iris around the inner extremity of each cone. It will be convenient to designate these rings of pigment-cells "*irides,*" in conformity with the nomenclature of the older writers. There are, as a rule, five or six iris-cells around each cone. These send pigmented fringes outward over the cone and inward over the great rods. In many insects (Hymenoptera and Nematocerous Diptera) the outer set of fringes are replaced by rod-like prolongations of the iris-cells. Each cell has a single pigmented rod, which has a bright, highly refractive spherule at its outer end, immediately beneath the cornea. These may be called ciliary rods (figs. 31 & 32. *cb*).

I have found ciliary rods in all the Hymenoptera and Nematocerous Diptera which I have examined.

In the Dragon-flies the soft cone is surrounded by pigmented fringes. Amongst these there are from twelve to sixteen thread-like processes which are not pigmented; each terminates in a bright, highly refractive spherule, like that of a ciliary rod. These spherules form a ring around the cone immediately beneath the corneal facet. They are figured by Claparède *. I shall speak of these threads as "*ciliary threads.*"

The form and connexion of the ciliary rods and threads suggest the idea that they may be concerned in regulating the amount of light which passes through the apex of the cone by means of a local mechanism. The action of light on the highly refractive particles possibly gives rise to a contraction of the iris. Whatever the mechanism by which the size of the aperture in the iris is regulated, it is certain that it is contracted in a bright light and dilated in the dusk, in nocturnal insects at least.

In Moths the well-known luminous reflex of the eye after the insect has been kept for a time in darkness is undoubtedly due to reflection from the spindles, as these are surrounded, in them, by numerous very close parallel tracheal vessels, which form a very perfect reflector. The disappearance of the reflex in the light is certainly due to the contraction of the irides. The gradual contraction of the bright field in each lenticulus of the cornea can be observed by means of a modification of the ophthalmoscope which I devised and shall hereafter describe.

It is a remarkable fact that the irides of the peripheral segments of the dioptron close before those of the central portion when the light falls directly in the axis of the latter, so that when the luminous eye of a moth is observed, it appears as if the bright part gradually became smaller until at last it entirely disappears.

Kühne is certainly mistaken when he says that the luminous reflex is of periodic recurrence †, and cannot be produced in the day. After exposure to a bright light the

* *L. c.*

† W. Kühne, "Observations on *Notodon* and *Acherontia*," Untersuch. Phys. Heidelberg, Bd. i. p. 242.

irides are often a very long time before they dilate, but I have never failed to see the reflex after the animal has been kept in the dark for half an hour, although it disappears almost instantly even in diffused daylight.

In the flies (Muscidæ) the cone is surrounded by four large flat cells, which extend from the margin of the cornea to the iris. All trace of ciliary rods and threads is wanting, although the irides are well developed.

The inner layer of pigment-cells is in immediate contact with the basilar membrane; the cells form rosettes around the inner extremities of the spindles, and send pigmented thread-like processes over their surface. In the Dragon-flies these cells give off a number of pigmented fringes which perforate the basilar membrane, and communicate with similar fringes from the pigment-cells of the neuron.

In the flies and in some Hymenoptera an intermediate set of stellate pigment-cells exists (pg^2) between the inner and outer pigment-cells of the dioptron. These cells intercommunicate with each other, and in some preparations this gives the great rods the appearance of branching and uniting with each other. I think that this appearance is usually deceptive: the spindles are certainly always distinct, but appearances in sections of the eye of the Lobster, and in some osmic-acid preparations of the eye of a Moth (*Hemerophila perfumaria*), certainly indicate that the sheaths of the spindles do intercommunicate in some parts of the eye.

I shall conclude my description of the dioptron with an account of some of the modifications in its several parts which I have observed in different insects, and I shall add what I am able concerning their development.

I feel that in many particulars this account will be somewhat incomplete, especially with reference to the development of the several structures; but I am unwilling to delay this communication for a fuller investigation, which will certainly occupy several summers at least.

A. *Modifications of the Cornea and Lens.*

The compound cornea exhibits four distinct types in insects, three of which are seen in the various stages of development in the eye of the Common Cockroach. All these are also found in the perfect condition in other Arthropods. In the earliest stage of development in the larval Cockroach the cornea is simple and continuous, without a trace of facetted structure. In this condition it consists of several transparent cuticular layers (figs. 75 and 76. *c*). The entire cuticular cornea is shed with each ecdysis, and is renewed from a layer of cells which, prior to the ecdysis, is situated between the old cornea and the cone. I believe that the new cuticular cornea is formed beneath, and not on, the surface of this cellular layer. In a larva of a Dragon-fly (*Agrion*), half an inch long, I found a layer of large flat hexagonal cells covering the whole surface of the cuticular cornea, one cell corresponding to each segment of the eye. These cells were firmly united to each other by their edges, and each contained a large lenticular nucleus.

In a section of this cornea the cuticular layers are seen to be very numerous, and they lie beneath the cellular layer. The nuclei of the cells stain very readily with eosin, whilst the remainder of the cornea remains unstained. The outer cellular layer is usually

absent when the cornea is continuous and without facets. I suspect it is shed after the development of the cuticular layers beneath.

I have named this type of cornea the *simple non-facetted cornea.* It is apparently the permanent condition in *Gammarus* and *Branchippus* amongst the Crustacea.

The second type of cornea (fig. 30) is seen in the functionally active eye of the larval Cockroach. It is divided into lenticular facets. I shall speak of this type as the *facetted cornea.*

The facetted cornea exhibits two distinct layers—an outer nuclear layer and an inner laminated layer.

This form differs from the continuous cornea in the persistence and further development of the cellular layer. The large flat nuclei of the cells enlarge at the expense of the cell-substance until they form the whole surface of the cornea, one nucleus forming each facet. This layer, when fully developed, is very hard and brittle. It is no longer stained by eosin, as in its semideveloped condition, but assumes a yellow colour in specimens which have been treated with chromic acid or its salts.

The structure of the facetted cornea is worthy of study in dried insects. I have a beautiful section from the eye of an African Carpenter Bee (fig. 30). The lenticular nuclei are firmly cemented together, and exhibit no trace of minute structure. The laminated portion beneath these consists of from fifty to sixty layers. These follow the contour of the inner surface of the lenticular facets.

Fine lines are also seen running perpendicularly to the laminæ. These correspond to the divisions between the facets. There are also distinct lacunæ between the laminæ, with minute teeth on each side of the lacuna; indicating that the laminated structure is probably due to the existence of finely serrated fibres interwoven with each other.

The third modification of the cornea in the Cockroach is only seen in the final stage of development: I shall speak of it as the *kistoid cornea* * (figs. 3 & 10).

I have not met with any description of the kistoid cornea, although it is preeminently characteristic of the most highly differentiated forms of compound eye. It consists of a chitinous (?) cuticular membrane folded on itself so as to resemble a piece of honeycomb, the openings of the hexagonal cells being turned inwards. The closed ends of the cells are segments of spheres: these form the surface of the cornea.

The hexagonal walls of the cells are often highly chitinized and deeply pigmented; the curved ends which form the corneal facets are thin, membranous, and very transparent. The material of which they are formed is usually soft, flexible, and elastic, and the two surfaces of the membrane are parallel to each other.

The cavity of the corneal cell is occupied by the oil-like lens which I have already described.

This lens is certainly developed from the substance of the cornea. I was fortunate enough to obtain sections of the eye of a Blow-fly which throw light upon this point. Fig. 15 shows three segments of the dioptron of an immature imago, which had not long before escaped from the pupa.

* Κίστη, a capsule or small case.

Each corneal facet consists of a chitinous membrane overlying a soft substance which is easily stained with logwood or carmine solution.

As development progresses the deeper portion of the cornea becomes more highly refractive, and loses its property of taking up stains. It appears as if the albuminous substance of the young cornea becomes gradually converted into a stroma infiltrated with oil. I have never seen the oil in drops, like those in a young fat-cell. In the rudimentary lens it appears rather as if the oil were evenly distributed throughout the whole substance of the lens.

In the condition which I have just described I have seen no traces either of division of the albuminous portion of the cornea into four, or of four nuclei; but in a still earlier stage there are distinct indications of four nuclei in each corneal facet, and in a later stage the appearance of the "nuclei of Semper" on the addition of ether, or by drying, points to the origin of the corneal lens from four original cells.

In the immature insect, during the development of the eye, a number of capsules, filled with cells containing an abundance of oil in large drops, are seen under the membrana basilaris. Similar cells are shown in some of Claparède's figures, and are named by him basal cells *. These are entirely absorbed during the development of the eye, and it appears probable that they afford the oil required for the formation of the refractive media. I have no doubt they belong to the system of fat bodies in which the larvæ and pupæ of insects are so rich.

The fourth form of cornea is apparently confined, amongst insects, to the imago form of some Gnats, but is also probably the condition in *Mysis*, in its perfect state, and in some other Crustacea. I propose to distinguish this type of cornea as the *lenticular cornea.*

The lenticular cornea consists of a number of well-developed, almost hemispherical lenses, which are nothing more than the united crystalline cones of the larva and nymph.

Dr. Grenacher has correctly figured and described the eye of the larva and pupa of a Gnat; but he adds: "I have only studied the eye of this insect (*Corethra plumicornis*) in the larva and pupa, not in the imago;" and says, "This is a matter of no importance, as the eye undergoes no change in passing from the pupa to the imago" †. I was at once struck by this remarkable statement, as the eye is covered by a smooth non-facetted cornea in the nymph, whilst the corneal facets in the imago are remarkable for their size and very great convexity (fig. 74)—a fact well known to all who have made the most cursory examination of the compound eyes in this family of insects.

A comparison of a section of the eye of the adult larva (fig. 76) or nymph (fig. 75) with that of the imago (fig. 74) shows that the great convex facets of the cornea of the perfect insect are really the ovoid crystalline cones ("*spherocones*") of the larva, covered by a thin cuticular membrane, which dips down between them, as the membrane of the kistoid cornea dips between its lenses.

In some of the Gnats the outer nearly hemispherical segment of the cone becomes converted into a nearly globular oil-lens, exactly like the oil-lens of a Crane-fly. The

* *L. c.* † *L. c.* p. 94.

inner segment of the cone then bears the same relation to the other refractive structures that the cone bears in the ordinary Diptera and Hymenoptera, or in insects and Crustaceans generally.

The formation of a fluid lenticulus from the substance of the cornea is not confined to the compound eye, but is also seen in the very different simple ocelli of some Arachnids. In a section of the simple ocellus of a Spider (*Salticus scenicus*) (fig. 34), which I prepared in the usual way and mounted in Canada balsam, the corneal lens is absolutely hollow. It evidently contained a fluid during life.

The sudden scintillations, which the bright reflex of the fundus of the eye of this insect exhibits in the living state, seem to indicate a power of accommodation, possibly from the action of muscle fibres which are inserted around the edge of the cornea.

Dr. Landois * traced the development of the subcorneal lens in the compound ocellus of a Caterpillar to a very different source. Soon after an ecdysis he found three spheroidal bodies very similar to those which I have described as a tetrasome in the eye of a larva of *Acridium* †. These unite to form the lens.

From the manner in which the cornea is formed in Gnats, I think it probable that this subcorneal lens becomes the cornea at the next ecdysis, and that a new lens is then formed from subcorneal cells or nuclei. Although I have not observed either subcorneal nuclei or cells in the eyes of caterpillars, both are very frequently seen in the eyes of larval insects.

I suspect that the compound cornea is developed in a similar manner in some Orthoptera, from the indications I observed in *Acridium*, but I am uncertain on this point; neither can I do more in the case of the Isopods than point out the very strong resemblance of the subcorneal lenses to those of the compound ocelli of caterpillars.

B. *Modifications of the Crystalline Cone.*

The outer portion of each segment of the dioptron, between the cornea and the external layer of pigment, may be conveniently termed "*the chamber*" (fig. 10 *ch.*). It is formed by the cuticular sheath of the segment, often thickened by a deposition of chitin; and is lined by fringes, pigment-cells, or ciliary rods.

The chamber contains the crystalline cone (*cc.*), which in many insects is replaced by a coagulable fluid, contained in four vesicles, and in others by four nucleated cells. Dr. Grenacher ‡ classifies the eyes of insects in three groups: those with a cone he calls *euconic*, those with the albuminous fluid *pseudoconic* §, and those with four nucleated cells *aconic*.

Up to a certain point my observations correspond with those of this distinguished author. In all insects the contents of the chamber are developed from four primitive cells ‖. This condition persists in the Crane-flies (*Tipula*), even in the recently formed imago (figs. 10 & 77); but I have failed to find these cells in the perfectly developed insect, in which the chamber is filled with an albuminous fluid, and I believe that the presence of the four nucleated cells is always evidence of immaturity. Dr. Grenacher's

* Zeitschr. für w. Zool. Bd. xvi.

† *L. c.* Phil. Trans.

‡ *L. c.*

§ Hydroconic, mihi, *l. c.* Phil. Trans.

‖ This was observed by both Claparède and Weismann.

pseudoconic type is, according to him, confined to the Diptera with short antennæ. In this, again, I cannot agree with him, as the Dragon-flies exhibit precisely the same conditions, and in the imago of the Cockroach I find a similar semi-fluid cone. In all these osmic acid coagulates the fluid, and even the eyes of flies exhibit a well-marked cone when the preparation has been so preserved (fig. 28).

The elongated cones which have been observed in the eyes of many Arthropods, extending from the cornea to the membrana basilaris (as, for example, in *Hyperia* *, *Typhis* †, and some other genera ‡), appeared to me for a long time to present great difficulties with regard to the views which I now hold. Further investigation has convinced me that these cones are artificially produced by the coagulation and drying of the albuminous tissues of the cone and spindle, with their cellular sheaths. The evidence of this is seen in numerous specimens of the eye of the Cockroach. In some of these there are distinct elongated cones, whilst in others more successfully prepared the spindle is well seen, and has the same form and structure as it exhibits in *Notonecta* and *Tipula.*

The crystalline cones of the Nocturnal Lepidoptera and of the higher Crustacea are probably morphologically distinct from the structures already described. The highly refractive cone in Nocturnal Lepidoptera is surrounded by a softer, or even fluid, sheathing cone, which extends from the apex of the crystalline cone to the spindle (figs. 3, 26, & 27, *sh*). I regard it (the sheathing cone) as the representative of the cone in the Diptera and Dragonflies.

Both the hard cone and its soft investing substance are divided into four longitudinal segments, indicating their origin from the four cells of the primitive cone; but I cannot at present decide whether the hard cone is formed from the inner portions of these cells or between them, as Claparède § thought not improbable.

In both Noctuid and Crepuscularian Moths, the optical transverse section of the cone often appears to contain four groups of deep purple granules; these, in optical longitudinal sections, are seen to lie on the surface of the cone, and are probably deposited by the decomposition of the fluid which surrounds the cone. In dried as well as in balsam-mounted specimens the sheath is so closely applied to the cone that it appears to form its outer portion, and the coloured granules therefore look as if they were imbedded in the substance of the cone itself ‖. Unicellular organisms are not infrequently found in the fluid contents of the sheath of the cone: these are undoubtedly parasitic (fig. 27, *z*).

It is by no means easy to understand the contents of the chamber in the Diurnal Lepidoptera in such genera as *Colias* and *Vanessa,* although in *Pieris brassicæ* no difficulty exists, the cone being similar to that of a Noctuid Moth. I have already figured the remarkable modifications seen in the two former genera ¶. I suspect that the cells (*c. c.*) in my figure are the representatives of the cone; and that the tetraphore is the outer extremity of the spindle, which retains its ovoid form after the escape of the fluid contents of the tube, and that the tube forms a narrow stalk supporting the chitinized

* Claparède, *l. c.* † id. ‡ Leydig. § *L. c.*

‖ Perhaps the coloured beads which cover the cone in *Notonecta* have a similar origin.

¶ Phil. Trans. *l. c.* fig. 35.

outer portion of the organ, which does not collapse like the rest of the spindle. This view is supported by a comparison of the outer end of the spindle in the Fly (fig. 19) with the structure in question.

C. *The Great Rods.*

The great rods consist essentially of the spindles and their cellular sheaths. The more important modifications of these structures have already been described, in their relation to the alterations which they undergo after death, and I have nothing to add further with regard to the very remarkable modifications which have been described by myself and others, except that they result from *post-mortem* changes.

The most important point in relation to the theory of Arthropod vision is, however, the direction of the axes of the great rods. It is well known that these are often seen to be strongly curved, even in the most carefully prepared sections, and this fact has been brought into prominence by the opponents of Müller's hypothesis *. Such a curved condition of the rods and spindles would be still more fatal to my own view. I have therefore carefully investigated this point, and conclude that this curvature is the result of changes of tension in the parts of the dioptron, and of the elasticity of the spindles. Sections made through the entire eye, immediately after the death of an insect, show no such curvature of the axes of the great rods when examined as opaque objects with low powers; yet the eyes of the same species exhibit very strongly curved rods when sections of the eye are examined in balsam. The manner in which the isolated rods twist and curl in all fluids shows that they must be powerfully affected by the action of the fluids usually required for the preparation of sections, and their action could scarcely fail to produce contortion of the great rods, even in the closely packed condition in which they exist in the cavity of the dioptron. The curvature would chiefly affect those rods which are nearest the periphery of the eye—a condition seen in all the sections which I have examined. The slightest pressure on the cornea in the recent eye permanently distorts the great rods. Hence it can hardly be expected that the axes of these structures would be undisturbed, at least around the periphery of the eye, in specimens preserved in any fluid which affects the normal tension of the parts.

I have made numerous attempts to determine the optical relations of the dioptric structures of the compound eye by means of a modification of the ophthalmoscope, but at present I have not been able to throw any further light upon the functions of the great rods by this means; except that the colour of the reflex obtained appears to depend on the colour of the fluid contents of the spindle.

I have found the best method of examining the reflex to be the substitution of a reflecting ophthalmoscope for the eyepiece of a microscope. By this means a bright luminous spot may be observed as a real image in the tube of the instrument. A quarter objective must be used, and the mirror of the ophthalmoscope must be strongly illuminated. The microscope is then focussed so that a real image of the corneal facets is seen between the objective and the eye of the observer. By bringing the object-glass gradually nearer to the insect's eye the reflex will come into view.

* Exner. Biolog. Centralblatt, i. p. 273.

The reflex appears as a disk having a fiery glow in Moths, and as a bright ruby spot in the Cabbage Butterfly. Sometimes six spots, surrounding a central spot, are seen in the eye of this insect: perhaps these are diffraction-images. A similar appearance is seen when the eye of this insect is observed by the naked eye, except that the spots are black. The central spot is always opposite the eye of the observer, whatever the position of the eye of the insect.

The reflex seen with the micro-ophthalmoscope is green in *Tipula* and bright yellow in the Diurnal Flies. Coloured diffraction-fringes are usually present around the central bright spot in both these insects; but the central image is sometimes surrounded by a perfectly black ring.

The manner in which the luminous reflex scintillates is very suggestive of an alteration in the focal plane of the dioptric structures under the control of the insect.

II. The Anatomy and Functions of the Neuron.

The neuron consists of a large nerve-papilla, or of a series of papillæ, which arise from the side of the procephalic ganglion, and form a retinal expansion on the inner or neural surface of the membrana basilaris (figs. 41 to 67).

The neuron may be conveniently divided, for purposes of description, into three parts —the retina (*rt.*), the optic nerve (*no.*), and the optic ganglion ($g.^1$) (fig. 41).

The retina consists of a layer of bacilla, supported by a complex neuroglia (fig. 56).

The bacilla present an inner (*i.*) and an outer segment (*o.*, fig. 53), like those of the rods and cones of the vertebrate retina. Both the inner and outer segments are very easily destroyed, and these structures are best examined by teasing out the recent retina in a very dilute solution of osmic acid, ·05 per cent.

The outer segments are cylindrical or conical, highly refractive, easily stained by chromic acid and its salts, but unaffected by logwood. In the Dragon-flies the outer segments often split into transverse disks.

The inner segments are protoplasmic, and are easily stained with logwood and carmine. They are richly supplied with very fine tracheal vessels (fig. 53). The inner and outer segments are of nearly equal length, and measure from 25 to 50 micromillimetres each. The outer segments are usually about 2^{μ} in diameter, and the inner are somewhat thicker.

The bacilla are usually arranged in bundles, which are bound together by the neuroglia, each bundle corresponding to a segment of the dioptron. In the Cockroach and the Blow-fly I have occasionally found some of the bacilla with the outer segment double, like the twin cones of fishes (figs. 65 & 66); and in some of the bacilla from the latter insect I have occasionally observed a lenticulus (fig. 64) between the inner and the outer segments. This is not stained by osmic acid, and closely resembles the lenticulus described in some vertebrate rods. I have never observed anything like the coloured globules of the cones of birds and reptiles.

The inner segment is usually finely granular, and is continued inwards as the axis-cylinder of a nerve-fibre.

The most remarkable modification of the bacilla is the separation of the inner and

outer segments in many larval forms, in the imago of *Tipula* and in most Noctuid Moths. In these cases a long fine axis-cylinder passes from the outer to the inner segment (figs. 46, 55, 57, & 67).

In the Noctuids a tracheal network is interposed between the inner and outer segments of the bacilla, permeated by the fibres which connect them with each other. The tracheæ form a kind of tapetum behind the outer segments.

A similar separation of the inner and outer segments of the bacilla occurs in the simple eyes of an Arachnid (*Phalangium*), which has been figured by Dr. Grenacher *.

It will be observed that the outer segments of the bacilla, which correspond in character with the outer segments of the vertebrate rods, are turned towards and not away from the refractive media. In this they conform to the usual condition in the invertebrate eye. I regard this as of developmental rather than of functional importance.

The outer ends of the bacilla are separated from the basilar membrane by a layer of fine branching endothelial cells. These are frequently pigmented, and send pigmented fringes inwards, which closely embrace the outer segments of the bacilla. The pigment is not deposited between the bacilla and the membrane, but only around the bacilla. I regard this layer as the analogue of the retinal pigment. It is always black. The pigment is entirely wanting in the Diurnal Flies, but is very abundant in the Lepidoptera, Hymenoptera, and Neuroptera.

The neuroglia of the retina consists of fine fibres (fig. 56), connected with the basilar membrane and with two distinct layers of small stellate cells—an outer layer between the outer and inner segments of the bacilla (a), and an inner layer at the inner extremities of the inner segments (m^2). In many specimens a number of small granules are seen crowded together between the outer segments of the bacilla (fig. 59). I am not certain of their nature, but it has occurred to me that they are possibly the broken outer ends of the bacilla themselves.

Sometimes large soft granular cells are seen in the same position (fig. 58). I think these are an indication of immaturity.

None of my predecessors in this investigation have described the bacilla. It may, therefore, be fairly asked, If these structures exist, how is it that they have been so frequently overlooked?

I think the answer to this question is found in the fact that it is only in very thin sections, such as they had not the means of preparing, that the bacilla can be recognized. In all ordinary sections a thick band of pigment between the membrana basilaris and the optic nerve is all that can be made out. When I wrote my former paper I had only seen the inner segments of the bacilla in the Flies, and I described them as a fascelloid layer †. I did not then understand their significance, and I had been working at the compound eye for over three years before I prepared a section which enabled me to recognize these structures as the terminal organs of the optic nerve.

Again, although the structure of the great rods has been very carefully investigated, that of the neuron has had very little attention paid to it. Even Dr. Grenacher, in his

* *L. c.* fig. 15. † *L. c.* Phil. Trans.

elaborate work, only represents portions of it in six figures; and these are all diagrammatic outlines, with but little detail.

M. Berger *, who has given the best figures and descriptions, has only worked with comparatively thick sections with low powers, and has not only overlooked the bacilla, but many other very obvious details.

On the other hand, it must be confessed that many observers have believed that they have traced nerve-fibres from the optic nerve into the great rods or their spindles. Dr. Grenacher has given one figure, and only one figure, in which he shows this relation. It represents three of the segments of the dioptron of a Crane-fly †; and in one of the three he has shown a nerve passing through the cuticular membrana basilaris, and ending in one of the cells of the spindle. I have occasionally observed an appearance similar to that represented in this figure, and my observations have led me to the conclusion that the fibres represented are not nervous, but form a portion of the connective framework. In *Tipula* the bacilla beneath each segment of the dioptron are enclosed in a distinct sheath (fig. 57), which often appears to be continuous with the sheath of the great rod. This gives rise to an apparent continuity between the neural and dioptric structures in many sections, and may have led Dr. Grenacher to believe that he had actually traced the nerve into the spindle.

There is no other figure in Dr. Grenacher's work which shows any actual passage of a nerve-fibre into the great rods; but two figures represent nerve-fibres passing up to, but not through, the basilar membrane ‡. These are both from the eyes of Crustaceans, in many of which the bacilla are very short. Several figures, of the eyes of Crustacea, actually show the bacilla, although the author has not referred to these in the text. In all the other figures, either the neuron is unrepresented, or it is only shown in outline without sufficient detail.

The retinal layer in Arthropods exhibits two very distinct modifications, which I propose to term the *segregate* and the *continuous retina.*

The segregate retina is characterized by having the bacilla arranged in distinct retinulæ, one for each segment of the dioptron. Each retinula is connected with the ganglion by a distinct fasciculus of nerve-fibres enclosed in a separate pigmented sheath (fig. 57). This form of retina is very frequent in larval insects; it is less often seen in the perfect state. The Crane-flies and some beetles have a segregate retina in the perfect condition: *Telephorus* affords a good example.

The continuous retina consists of a bacillary layer extending over the inner surface of the basilar membrane, connected with the ganglion by a single large nerve-trunk, the fibres of which exhibit a complete decussation (figs. 41, 51, *rt*). The bacilla always, however, show a tendency to be collected in small bundles, one corresponding to each segment of the dioptron, except in some of the Dragon-flies, wherein the central portion of the bacillary layer, at least, does not exhibit any division into separate fasciculi.

The continuous retina is characteristic of the true Flies (Brachycerous Diptera), of some Hymenoptera, Lepidoptera, and Neuroptera.

* E. Berger, " Untersuch. u. den Bau des Gehirns und der Retina des Arthropoden," Arb. Zool. Inst. Wien, tom. i. (1878). † *L. c.* fig. 44. ‡ *L. c.* figs. 109, 114.

In many perfect insects, and in some stages of development in others which in the perfect form have a continuous retina, conditions exist which are intermediate. For instance, the bacillary layer may be continuous, but the optic nerve split into numerous separate bundles; or the segregate retina may consist of fasciculi so closely united that it is difficult to decide to which form the modification should be assigned. These variations are of developmental significance, as will be shown hereafter.

The fibres of the optic nerve are medullated, although in most preparations all traces of the medullary sheath are lost. It is not, however, difficult to make out the sheath in recent specimens fixed with osmic acid. I now consider the varicose appearance of the axis cylinders which I formerly described to be due to *post-mortem* changes *.

The arrangement of the fibres in separate fasciculi in some insects has already been alluded to. When they form a single nerve-trunk most sections exhibit the complete decussation of the nerve-fibres. In some planes, however, the only indication of such an arrangement is the cut ends of many of the nerve-fibres. Such variations are undoubtedly due to the plane of the section.

When the retina is segregate, the nervous bundles, which unite the retina with the ganglion, do not decussate; but in this case a deeper layer of decussating fibres can usually be seen in the substance of the ganglion itself (fig. 44).

Supporting fibres connect the inner surface of the retina with the outer surface of the ganglion, when the nerve consists of a single trunk (fig. 56, *d*).

The retinal ganglion is spread over the surface of the optic lobe (*op.*) of the cephalic ganglion (figs. 48 & 49).

It usually exhibits at least four layers, although the number is sometimes greater.

In the Fly (fig. 56) the outer layer (*f*) consists of small round nuclei imbedded in a finely granular matrix. The matrix is permeated by fibres connected with a layer of stellate cells (*g*), which lie in the central zone of the next layer.

The second layer, beside containing the stellate corpuscles just alluded to, is chiefly made up of large fusiform cells (cl^1), which are connected at both their extremities with fine fibres. The third layer of the ganglion consists of a number of very fine fibres (*h*), which run parallel to the surface of the ganglion. The supporting fibres of the first and second layers spread out into foot-like disks on the surface of the fibrous layer (*i*). The fourth layer (cl^2) resembles the second, except that I have not detected any stellate corpuscles in connexion with its supporting fibres.

The retinal ganglion is connected with the deeper portions of the optic lobes by fibres (no^2), between which a large number of tracheal tubes lie. These supply the fine tracheal vessels of the ganglion itself.

In the ganglion of the retina in *Agrion* (fig. 42) there are two extra layers within the inner cellular layer—a second layer of fibres parallel with the surface of the ganglion (f^2), and a second nuclear layer (n^2); and the ganglion is connected with the deeper structures of the nervous system by a second layer of decussating fibres (*x*).

In *Tipula* and the Gnats the structure of the ganglion is not so complex. In these

* Phil. Trans. *l. c.* p. 585.

insects (fig. 57) I have been able to make out only two layers—a nuclear layer (*nuc*) and a layer of large fusiform cells (*cl*). The latter are connected by a number of nearly parallel nerve-fibres (no^2) with a deep ganglionic layer, which consists of small stellate cells (*g*).

III. On the Development of the Compound Eye.

The dioptron and neuron are developed from two distinct sources: the former originates from the hypodermis, the latter from a solid outgrowth of the cephalic ganglia; so far, therefore, there is ground for a morphological comparison between the nervous and dioptric structures of the vertebrate and compound eye. The dioptron is comparable with the crystalline lens, whilst the neuron, so far at least, is homologous to the retina.

The researches of Dr. Weismann * have shown that the dioptron in the Fly is formed from a single layer of cells, and my own observations verify this in the case of the Lepidoptera and the Dragon-flies.

It is well known that the outer facets of the eye in the Crustacea are developed later than the more central facets, the eye increasing in magnitude with each successive ecdysis. But I do not know that it has been remarked that the peripheral portion of the eye in insects is less developed than the more central part. I have found this to be the case even in the fully formed imago, whilst a section taken through the eye of an immature imago often throws much light on the manner in which the eye is developed.

In larvæ in which the compound eye is functionally active such sections are still more instructive.

Perhaps it is by the gradual addition of fresh facets that the segregate retina takes its origin. In the Dragon-flies, at least, the continuous retina of the imago is not fully formed until after the final ecdysis, when it gradually replaces the segregate retina of the larva.

The dioptron in its earliest stage of development consists of a single layer of columnar cells, which cannot be distinguished from the ordinary hypodermis of the insect. I have observed this condition in various Lepidopterous larvæ. The columnar cells lie immediately beneath a continuous non-facetted cornea.

At this stage numerous tracheal vessels and stellate cells lie beneath the columnar layer, and processes from the columnar cells pass into the deeper layer, where they communicate with the stellate cells, which belong to the ordinary connective tissue of the insect.

In this respect the columnar cells closely resemble the cells of the sensory epithelium in the Medusæ and Mollusca. The researches of the brothers Hertwig † show that in the Medusæ the cells of the sensory epithelium, in the region of the rudimentary eye-spot, become the terminal organs of the nerve. This may possibly be regarded as an indication in favour of the hitherto accepted view that the sensory terminations of the nerve in the Arthropod are developed from the hypoderm. Such a conclusion is, however, in my estimation, no more justified than if it were extended to the case of the crystalline lens of a vertebrate. In the Medusa the epithelial cells, from which the

* Zeitschr. f. w. Zool. Bd. xiv.

† O. und R. Hertwig, Das Nervensystem und Sinnesorgane des Medusen.

nerve-terminals are believed to be developed, are those of an undifferentiated epiblast; whilst in the Arthropod, as in the vertebrate, the great neural tract has already been differentiated before the groundwork of the compound eye is laid in the cells of the hypoderm Metschnikoff *. The hypodermic cells in the region of the dioptron become greatly elongated, and undergo both longitudinal and transverse subdivision; but as the tracheal vessels and stellate connective-tissue cells permeate the hypoderm at a very early stage in the development of the dioptron, it is extremely difficult to determine how much of this structure is derived from the hypoderm and how much originates in mesoblastic elements. The earliest stages of development are far more difficult to follow in the Diptera. This arises from two principal causes: first, the "imaginal disks" from which the integumental structures of the imago are developed are closely united to the nervous system; and secondly, the whole development is very rapid, and the parts are exceedingly soft and easily destroyed.

The compound eye of the larva of *Corethra*, in the earliest stage in which I have yet observed it, closely resembles the same structure (as figured by Metschnikoff †) from *Aphis rosæ*. It consists of a discoid group of pyriform cells, with their long axes at right angles to the surface of the disk. The rounded outer ends of these cells lie immediately under the transparent non-facetted cuticle, which represents the cornea. Their inner extremities are prolonged, and are intimately connected with the deeply pigmented sheath of the optic nerve.

Dr. Weismann ‡ has figured the disk from a still younger larva, and shows the nerve ending in a layer of cuboid cells, which, from observations I have made on the very rudimentary eye of a Lepidopterous larva, form, I believe, a distinct layer beneath the disk from which the refractive structures are developed. My own observations have led me to conclude that at this stage the nerve-fibres end in a bed of granular nucleated protoplasm, not unlike a large motorial end-plate (fig. 73). Each of the pyriform cells of the disk has a bundle of rod-like bodies of an orange-brown colour near its outer end. These eventually develop the cone and spindle.

The rods are larger in the cells of the centre of the disk than in those of its periphery; and the whole cell shows symptoms of division into four longitudinal parts.

The close relationship of this disk to the cephalic ganglion, both in *Aphis* and *Corethra*, throws light upon the still more remarkable developmental history of the eye in the true flies, so well described by Weismann.

In these the disk is attached to the optic ganglion by a narrow pedicle, and has no connexion with the other integumentary structures in the pupa. It is one of the remarkable cellular expansions which are known as "imaginal disks." The head and thorax of the imago are formed from a series of these disks, which are really involutions of the epiblast. These are drawn into the interior of the embryo whilst it is yet inclosed in the egg.

The procephalic lobes and all the appendages of the head are distinctly seen as rudi-

* Zeitschr. f. w. Zool. 1871; Monthly Mic. Journ. 1872. † Zeitschr. f. w. Zool. Bd. xvi.
‡ Zeitschr. f. w. Zool. Bd. xiv.

ments in the embryo some time before the hatching of the egg; but before that event they are withdrawn into the interior of the embryo by a process of invagination during the formation of the fore gut, which lies entirely in front of these structures.

The fore gut forms no part of the alimentary canal of the imago, but is shed with the larval integument in the first stage of the formation of the pupa. This then puts on the same appearance as the embryo had whilst it still lay inclosed in the egg, by the unfolding of the imaginal disks; and these, again, form the anterior part of the body.

After the unfolding of the imaginal disks, the development of the compound eye proceeds in the same manner as in those insects in which it is developed from the cells of the hypoderm.

I believe that the pedicle, which supports the disk from which the dioptron is developed, is merely a portion of the connective-tissue capsule that incloses the ganglion before the evolution of the disks in the formation of the pupa. The optic nerve and retina are formed at a later period.

These facts throw light on the relationship between the ordinary compound eye and the remarkable encapsulated eye of the entomostracous Crustacean, *Leptodora hyalina*, described by Dr. Weismann †. This is deeply seated in the median line of the transparent head, in immediate relation with the cephalic ganglion, and it has no apparent connexion with the skin or surface of the animal.

In describing the variations of the retina I have already adverted to their developmental significance. I have especially studied the developmental relation of the segregate and continuous forms of retina in the Dragon-flies, and there are numerous indications that what I have actually observed in these insects is a common phenomenon amongst the Arthropods. In the earlier stages of the Dragon-fly larva the compound eye is already functional, at least as far as its central facets are concerned. In this condition there are very few facets. Those of the more central portion of the eye have a distinct retinula to each, and each retinula has a distinct nerve-bundle (figs. 43 & 45). As development progresses, new segments are added to the periphery of the dioptron, and the number of retinulæ increases.

In some sections the continuous retina of the perfect insect (*rt*) is already seen upon the surface of the optic lobe (fig. 44), and the fibres of the nerves from the partial retinæ (*rt**) can be seen passing between its rudimentary elements. The existence of a decussating nerve beneath the continuous retina is very apparent. The retinal ganglion (fig. 44, *g′*) is now deeply seated in the interior of the optic lobe.

Beneath the ganglion, both in this and in later stages, there is a remarkable ganglionic centre (marked *k* in my figures). It is in relation with the retinal ganglion by a second bundle of decussating fibres. It is, I believe, the representative of those remarkable kidney-shaped bodies described by Mr. Newton in his admirable description of the eye of the Lobster ‡.

As development progresses, the continuous retina gradually enlarges, and approaches

† Zeitschr. f. w. Zool. Bd. xxiv.

‡ E. F. Newton "On the Eye of the Lobster," Quarterly Journal of Mic. Science, 1873.

the inner surface of the membrana basilaris of the dioptron (figs. 41 & 45); so that at the final ecdysis it entirely replaces the partial retinæ of the larval eye.

This complete change of the larval retina at the final ecdysis is undoubtedly a very remarkable phenomenon. When, however, the epiblastic nature of the nervous system is borne in mind, it is not, perhaps, more remarkable that an ecdysis should occur in relation to the nervous than that it should occur in relation to the cutaneous epithelia. It has occurred to me that the kidney-shaped ganglia already alluded to, which apparently vary much in number in different stages of development, may be really successive rudimentary ganglia and retinæ destined in turn to become functional.

The extent of the final continuous retina varies much in different species of insects. In *Agrion* the whole inner surface of the basilar membrane is in contact with the continuous retina in the fully formed imago; but in the great eyes of *Æshnia* it only replaces the central retinulæ. The same partial replacement of the retinulæ is the condition in many insects in which the eye is only functional in the imago. In these it is probable that the central portion of the retina is continuous from its first formation, and that it is, as it were, supplemented by peripheral partial retinæ.

Most of the Lepidoptera apparently exhibit this condition, the continuous retina being most developed in the Diurna. As has been already stated, the larval condition is permanent in the Crane-flies and Gnats; whilst in the Diptera with short antennæ, Muscidæ and Tabanidæ at least, where the formation of the pupa almost partakes of metagenesis, no partial retinæ are ever formed. It appears as if the developmental processes had been much abbreviated in these insects, and that the final stage is reached by a single and complete metamorphosis.

IV. On the Morphology of the Eyes of Arthropods.

Although of late the views of Müller with regard to the relations of the simple and compound eyes of Arthropods have fallen into discredit, I must return to these views.

The eyes of the Isopod Crustaceans, which he spoke of as aggregate, are undoubtedly really intermediate between a simple and compound eye. The transition from a few widely separated simple eyes, which form the aggregate eye, is so natural that it has only obtained discredit because there is a wide difference in the structure of the stemmata of insects or Arachnids, and of the compound eye.

The case is, however, otherwise with the simple eyes of larval insects, which are almost identical with a segment of the dioptron of the compound eye. Landois *, describing the eyes of several caterpillars in 1866, remarked that they present a condition intermediate between that of the compound eye and the ordinary simple eye, and proposed the term "*ocelli compositi*" for them. I have figured sections of the eyes of three noctuid caterpillars (figs. 36–40); these exhibit a lens consisting of three segments placed immediately beneath the very convex corneal facet.

* Zeitschr. f. w. Zool. Bd. xvi.

The lens is not unlike the crystalline lens of a vertebrate. It is albuminous, or at least gives a characteristic yellow with nitric acid.

Beneath the lens a fusiform spindle is seen, very similar to the spindle of the compound eye. This has a retinula beneath it consisting of a small fasciculus of bacilla. Several of these eyes are united by a common optic nerve, like the stemmata of insects, and three usually form a group.

I believe that the spindle in this form of eye has the same function as that which I have assigned to it in the compound eye.

A comparison of the figures given by Dr. Grenacher * of the eyes of *Porcellio* and of *Sialis* larva with those of the ocelli of caterpillars which accompany this paper, will show how close the relation of these structures is to each other. On the other hand the absence of a subcorneal lens and spindle, as well as the arrangement of the retinal elements, in the simple ocelli of insects and arachnids, show that these organs are formed on a type which differs essentially from that exhibited by the compound eye.

I believe, however, that the columnar cells immediately beneath the cornea, the vitreous of Dr. Grenacher, represent the dioptron; they are undoubtedly of hypodermic origin, and are separated from the retina by a fibrous membrane which apparently corresponds to the membrana basilaris of the compound eye. Dr. Grenacher figures and describes this membrane † in a species of *Salticus*, and traces the fibres of which it is composed, from the outer ends of the bacilla of the retina to a number of nuclei situated in a sinus which surrounds its margin. I have made some remarkably good sections of the eyes of *Salticus scenicus*, in which it is quite easy to see that no such connexion exists between these structures.

In some of these sections the fibrous membrane has completely separated from the bacilla, just as the membrana basilaris separates from the retina in the compound eye.

The sinus (*ls*, fig. 33) which surrounds the membrane in *Salticus* contains radiating fibres very similar to those which I have described in the sinus around the margin of the membrana basilaris of the compound eye; and it is these fibres which contain the nuclei to which Dr. Grenacher believes he has traced retinal fibres.

At present the origin of the retina of the simple eye cannot be said to have been determined; I have sought in vain for any reliable indications as to its origin. Dr. Grenacher believes it to arise by a modification of the cells of the hypoderm ‡. His arguments in favour of this origin are very unsatisfactory, and apparently indicate that the vitreous and not the retinal elements arise from this layer.

A cellular vitreous is always present in the simple eyes of insects : I formerly failed to demonstrate it in the stemmata in Flies, but I have since found that this layer exists, although from its extreme thinness it is not easily seen except in specimens preserved with osmic acid §.

On this point, at least, I must endorse the views of Von Graber ||, rather than those of Dr. Grenacher. In a very able paper by Prof. E Ray Lankester and Mr. A. G. Bourne ¶,

* *L. c.* figs. 12, 95, 96, & 97. † *L. c.* ‡ *L. c.* § Phil. Trans. *l. c.*

|| Archiv f. mikrosk. Anat. vol. xvii. 1880, p. 58. ¶ Quarterly Journal of Microscopic Science, Jan. 1883.

the vitreous is said to be absent in the lateral eyes of Scorpions, although it is present in the more highly developed central eye. This is a remarkable exception to the conditions which I have observed; but as I formerly overlooked the vitreous in cases in which I now know it exists, I cannot help suspecting that the cells have been destroyed in some way in the preparation of the sections.

I propose the following classification of the visual organs of the Arthropoda.

I. Simple ocelli.	III. Aggregate eyes.
II. Compound ocelli.	IV. Compound eyes.

I. Simple ocelli.—I include under this term the ocelli of Arachnida and the stemmata of perfect insects, and I think it probable that the eyes of the Myriapoda consist of clusters of such stemmata; but at present I am not sufficiently acquainted with the modifications of the eyes of this family to speak with any degree of certainty, as the investigation of the eyes of Myriapods is exceedingly difficult.

II. Compound ocelli.—I use this term to indicate the ocelli of larval insects in which there is apparently a second refractive system—the spindle, which magnifies and erects the subcorneal image.

I have little doubt that the eyes of the *Coryceidæ*, at least those of *Copilla*, belong to this class; but I have not had any opportunity of examining them, and only judge from Dr. Grenacher's description and figures.

III. Aggregate eyes.—I include in this division the semi-compound eyes of Isopods, which appear to be nothing more than aggregations of compound ocelli.

Dr. Grenacher regards the subcorneal lens of the Isopod as a highly modified crystalline cone. I regard it as the representative of the oil-lens of the compound eye, and of the lens of the compound ocellus; perhaps the cone of the compound eye should also be regarded as a highly modified form of lens; at least it departs more from the primitive type than the spheroid lens of the Isopod.

IV. Compound eyes.—These are the ordinary eyes of the Crustacea and Insecta. They exhibit very various forms, and many efforts have been made to classify them, chiefly founded on the variation of the dioptron, and especially those of the cornea and crystalline cone.

All these classifications appear to me unsatisfactory from a morphological point of view, as they do not harmonize with the affinities of the forms of the Arthropods in which the variations occur, neither do they throw any light on the genetic relations of the compound eye.

Perhaps the following classification will be useful in making the relations of the various forms more easily comprehended.

I am so little acquainted with the structure of the eye in the Crustacea from personal observation that I shall confine my remarks chiefly to the conditions which I have observed in the Insecta.

(1.) Eyes in which the dioptron is *incompletely* separated from the neuron, each segment of the former having a distinct retinula. I have observed this condition in the larva of the gnats, in *Tipula* and in the genus *Telephorus* amongst the Coleoptera.

(II.) Eyes in which the dioptron is *completely* separated from the neuron by the membrana basilaris, but in which the retina *is divided into distinct retinulæ.* This is the condition of the compound eye of the Dragon-fly larva, in the imago of the Gnats, and in the Orthoptera.

(III.) Eyes in which the dioptron is *completely* separated from the neuron, and the retina *is continuous,* but in which the nerve-fibres of the optic nerve are arranged in *distinct* fasciculi : this condition holds in many Hymenoptera, Hemiptera, and Lepidoptera.

(IV.) Eyes in which the dioptron is *completely separated* from the neuron, in which the retina *is continuous,* and the fibres of the optic nerve *form a single bundle* and *decussate completely.* This condition is found in the Muscidæ, the Diurnal Lepidoptera, and in the perfect form of some Dragon-flies (*Agrion*).

It would appear therefore that the compound eye is to be regarded as a collection of *compound ocelli,* in which the tendency to close union is greater nearer to the surface than in its deeper portion, the optic nerves being the last parts to become fused into a single compound structure.

DESCRIPTION OF THE PLATES.

The small letters indicate the following parts in all the figures.

c. The cornea.
cc. The crystaline cone.
cn. Subcorneal nuclei.
ch. The chamber.
cb. Ciliary bodies.
$cl^1.cl^2$. Outer and inner cellular layers.
$g^1.g^2$. Sections of the optic ganglion.
h. Hypodermis.
i. Iris cells.
k. Deep or kidney-shaped ganglion.
l. Lens.
ls. Lymph-sinus.
m. Basilar membrane.
mc. Ciliary muscle.
$n^1.n^2$. Nuclear layers.
nuc. Nuclear bodies.
no. Optic nerve.
op. Optic ganglion.
pg. Pigment.
rf. Radating fibres.
rt. Retina.
*rt**. Partial Retinæ.
sh. Sheath of the great rods.
sp. Spindles.
sr. Scleral ring.
tv. Tracheal vessels.
v. Vitreous humour.

PLATE XL.

Fig. 1. A semidiagrammatic section of the eye and optic ganglion of a Blow-fly.

1 *a.* The membrana basilaris of the same insect seen from its neural surface. *ped,* pedicle of the scleral ring. Both figures show the large muscle *m.c.* attached to the inner edge of the scleral ring, *sr.*

2. A diagram showing the manner in which the image is formed on the Arthropod retina.

3. An optical section of two of the segments of the dioptron of the Plume Moth (*Pterophorus pentadactylus*).

4. A diagram showing the optical relations of the same.

5. A semidiagrammatic representation of a vertical section through the great eyes of a Dragon-fly (*Æshnia*), showing the lymph-channels ; *a.a.* afferent vessels ; *b.b.* efferent openings.

6. A section through the scleral ring and membrana basilaris in the region of the efferent lymph-path, showing the radiating fibres *rf,* from the eye of *Æshnia.*

7. A similar section from the eye of *Agrion.*

8. A section through the scleral ring, *s.r.,* of *Agrion,* showing a marginal lymph-opening.

9. The afferent vessels of the dioptron of *Æshnia.*

Fig. 10. An optical section of a segment of the dioptron of *Tipula* in the recent condition.

11. The spindle of the eye of the same, slightly altered by the process of preparation.

12. A similar spindle.

13. A segment or tube of a spindle from the same insect, showing the contracted tube with soft vacuolated material adhering to it, possibly a portion of its contents.

14. *a*. A transverse section through the spindle of the same insect.

14. *b*. A similar section, in which the peripheral tubes have partially collapsed.

15. Three of the peripheral segments of the dioptron of a Blow-fly in the immature condition.

16 to 18. Portions of the great rods of a Blow-fly, showing the different appearances which they present, owing to partial or total collapse of the spindle.

16. A portion of the spindle partially emptied by pressure.

17. A specimen showing still further collapse of the tubes.

18. A portion of a spindle showing vacuolation of the sheathing-cells and collapse of the tubes in normal saline solution.

19. The lens at the outer end of the spindle from the same insect, from an osmic-acid preparation; *nuc.* spheroids in the interior of the lens, *sp.* spindle.

20. A transverse section of the great rods, spindles, *sp.*, sheathing-cells *sh.*, and tracheal vessels, *tv.*, from the same.

21. The lens-capsule, ruptured by pressure, from the Earwig.

22. A single segment of the dioptron, and a few bacilla from the Yellow Underwing Moth (*Triphæna pronuba*), from a specimen prepared in chloral hydrate solution.

Plate XLI.

Fig. 23. A section through the entire eye of a Noctuid (*Xylophasia polyodon*).

24. Transverse sections through the cone of the same insect: *a*, near the base; *b*, near the apex, showing the coloured granules.

25. Transverse sections through the rods and spindles of the same insect: *a*, *b*, *c*, three successive sections through the spindle-sheath; *d*, section through the spindle showing the cells of the sheath; *e*, section through a stellate spindle.

26. The chamber and cone of the same insect. The tube has collapsed.

27. The tube between the cone and spindle, from the eye of a species of Noctuid Moth; the tube contains unicellular parasitic organisms, *z*.

28. The chambers and a portion of the spindles of two segments of the dioptron, an osmic-acid preparation from the eye of a Blow-fly: *oc*, outer portion of the cone; *cc'*, crystalline cone.

29. The spindle from the same, mounted in a dilute solution of osmic acid.

30. A section of the cornea of an African Carpenter Bee (*Xylocopa*), from a dried insect, showing its laminated structure: c^1, lenticular layer; c^2, laminated layer; c^3, inner surface.

31. A single segment of the dioptron of an Ant (*Formica rufa*), showing the ciliary rods *cb.*; 31 *a*, one of the ciliary rods detached and more highly magnified.

32. A similar preparation from the eye of a Wasp (*Vespa germanica*): 32 *a*, one of the same detached and more highly magnified; cb^1, refractive granule; cb^2, iris cell; cb^3, fringe-like process.

33. A portion of the eye of a Spider (*Salticus scenicus*), showing the fibrous membrane *m*, which separates the dioptric from the nervous structures; *ls*, lymph-sinus, containing radiating nucleated fibres.

34. Two of the eyes of *Salticus scenicus*.

35. The simple ocellus of a Blow-fly: 35 *a*, one of the retinal elements more highly magnified; r^1, outer refractive segment; r^2, intermediate pigmented portion; r^3, nucleated protoplasmic portion.

Fig. 36. One of the compound ocelli of a Noctuid caterpillar: *h*, hypoderm; *pg*, pigment covering the spindle.

37. One of the compound ocelli from another Noctuid caterpillar.

38. A similar preparation from a third species of Noctuid caterpillar: *no*, union of three nerve-trunks from three compound ocelli.

39. An oblique section through a similar eye in an embryonic condition.

40. A transverse section of a compound ocellus from a Noctuid caterpillar, showing the iris and lens *in situ*.

Plate XLII.

Fig. 41. A transverse section through the entire eye of a Dragon-fly (*Agrion virgo*), from the perfect insect.

42. A highly magnified representation of a portion of the retinal ganglion, from the same preparation: n^1, nuclear layer; cl^1, cellular layer; f^1, fibrous layer; cl^2, second cellular layer; f^2, second fibrous layer; n^2, second nuclear layer; *x*, second decussating layer of fibres.

43. A section through the entire eye of a larval *Agrion*, from a specimen 6 lines long: *rt**, segregate retina; g^1, ganglion.

44. A similar section from a more advanced larva.

45. A similar section from an adult larva.

46. The bacilla from the neuron of the same larva.

47. The bacilla from the neuron of a Dragon-fly larva (*Libellula depressa*).

48. The cephalic ganglia of a Cockroach, from a large larva, seen from behind: *op*, optic lobe; *n*, nerves to partial retinæ.

49. The same, seen from before.

50. A transverse section through one of the partial retinæ in a rudimentary stage: *no*, one of the optic nerves.

51. A section through the neuron of a Fly (*Syrphus ribesii*).

52. A portion of the retinal ganglion of the same, seen with an immersion lens $\frac{1}{12}$. (The references as in fig. 42.)

53. Two bundles of bacilla from the retina of the Blow-fly, from an osmic-acid preparation, showing the tracheal vessels and cells of the neuroglia : *o* outer and *i* inner segments.

54. A transverse section through the entire eye of a Gnat.

55. Bacilla from the eye of *Tipula*, showing the axis-cylinder between the inner and the outer segments.

Plate XLIII.

Fig. 56. A semidiagrammatic representation of the retina of the Blow-fly, drawn from preparations prepared in different fluids, and showing the connexions of the various elements: *a*, neuroglia of the retina, from a chloral hydrate preparation; *b*, the same, from an osmic-acid preparation; *c*, the bacilla, from osmic-acid preparations; B^1, outer segments; B^2, inner segments; *d*, the neuroglia of the optic nerve; *e*, the fibres of the optic nerve, from osmic-acid preparation; *f*, outer layer of ganglion, osmic acid; *g*, cells with the supporting neuroglia, chloral hydrate; *h*, transverse fibres, Müller's fluid; m^2, inner limiting membrane of retina; m^3, endothelium covering the ganglion; no^2, inner nerve-fibres connecting the optic and deep ganglion. The other references are the same as those in the rest of the figures.

57. A portion of the neuron of a Crane-fly (*Tipula oleracea*). The references as in fig. 56.

Fig. 58. A portion of the retina of a Blow-fly, from a specimen prepared with chloral hydrate, and stained with eosin.

59. A portion of the retina of the Blow-fly, osmic acid.
60. A portion of the retina of a Blow-fly, Müller's fluid.
61. A transverse section of a portion of the retina of a Blow-fly, from a specimen prepared with Müller's fluid and mounted in balsam.
62. A transverse section of a portion of the retina of a Blow-fly, through the inner segments of the bacilla, from a specimen preserved in chloral hydrate and subsequently mounted in balsam.
63. Two fasciculi of bacilla, from a Hawk-Moth pupa.
64. Bacilla of a Blow-fly, showing the lenticulus, from an osmic-acid preparation.
65. Bacilla from the eye of a Cockroach, with double outer segments.
66. Similar bacilla, from the eye of a Blow-fly.
67. Bacilla from the eye of a Noctuid Moth.
68. Tracheal vessels on the inner surface of the membrana basilaris of the Blow-fly.
69. Retinal pigment-cells and a portion of the basilar membrane of a Dragon-fly (*Æshnia grandis*).
70. A portion of the basilar membrane from the eye of a Lobster, showing prismatic thickenings at the inner extremities of the great rods.
71. A portion of the retina and basilar membrane of the Cabbage Butterfly, showing lenticular thickenings.
72. A vertical section through the basilar membrane of *Syrphus*, showing the cellular sheaths of the fasciculi of bacilla, and the cells around the necks of the expanded tracheal sacs of the dioptron.
73. The disk from which the retina originates, from a Lepidopterous larva (Noctuid).
74. Two segments of the dioptron, with their retinulæ, from the eye of a perfect Gnat (*Corethra plumicornis*) : 74 *a*. A transverse section through the inner extremity of the cone of the same; 74 *b*. A transverse section through the spindle of the same.
75. A portion of the dioptron of the larva of the same insect.
76. A section of a portion of the eye of a young Gnat larva.
77. A portion of the dioptron of an immature Crane-fly (*Tipula oleracea*), which had just escaped from the pupa.

NOTE.—Since the above was sent to press, my attention has been drawn to a short paper by Justus Carrière of Strassburg (Quart. Journ. of Micros. Sci. Oct. 1884, p. 673), "On the Eyes of some Invertebrata," in which my retinal layer is figured. He speaks of it as the "palisade layer." He remains, however, a disciple of established views, and has not given the retinal layer nearly so much attention as it deserves. So far as his observations go, they appear to me to confirm my own, as I firmly believe that M. Carrière, on further investigation, will be led to admit the validity of my views.

B. T. Lowne del.

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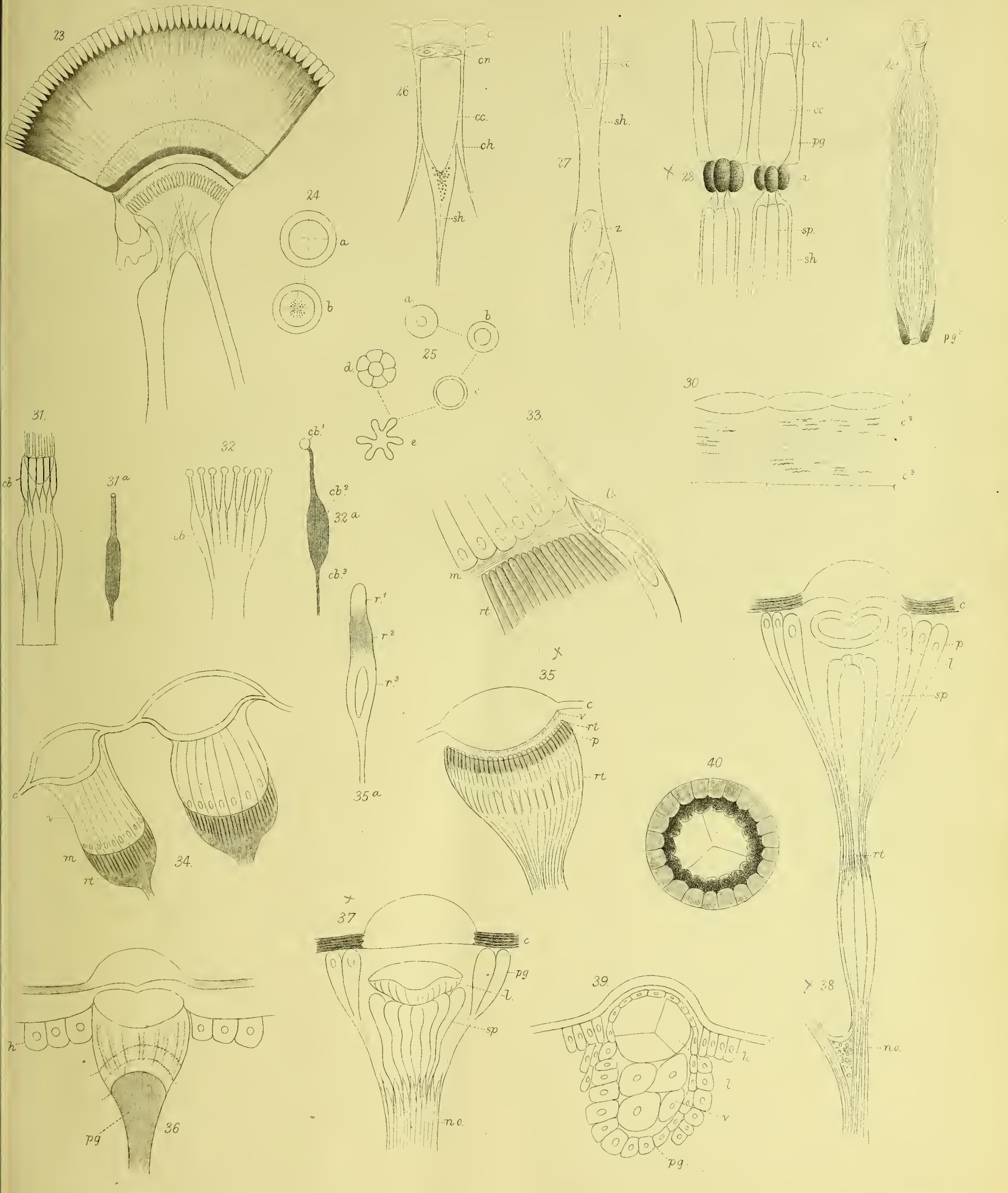

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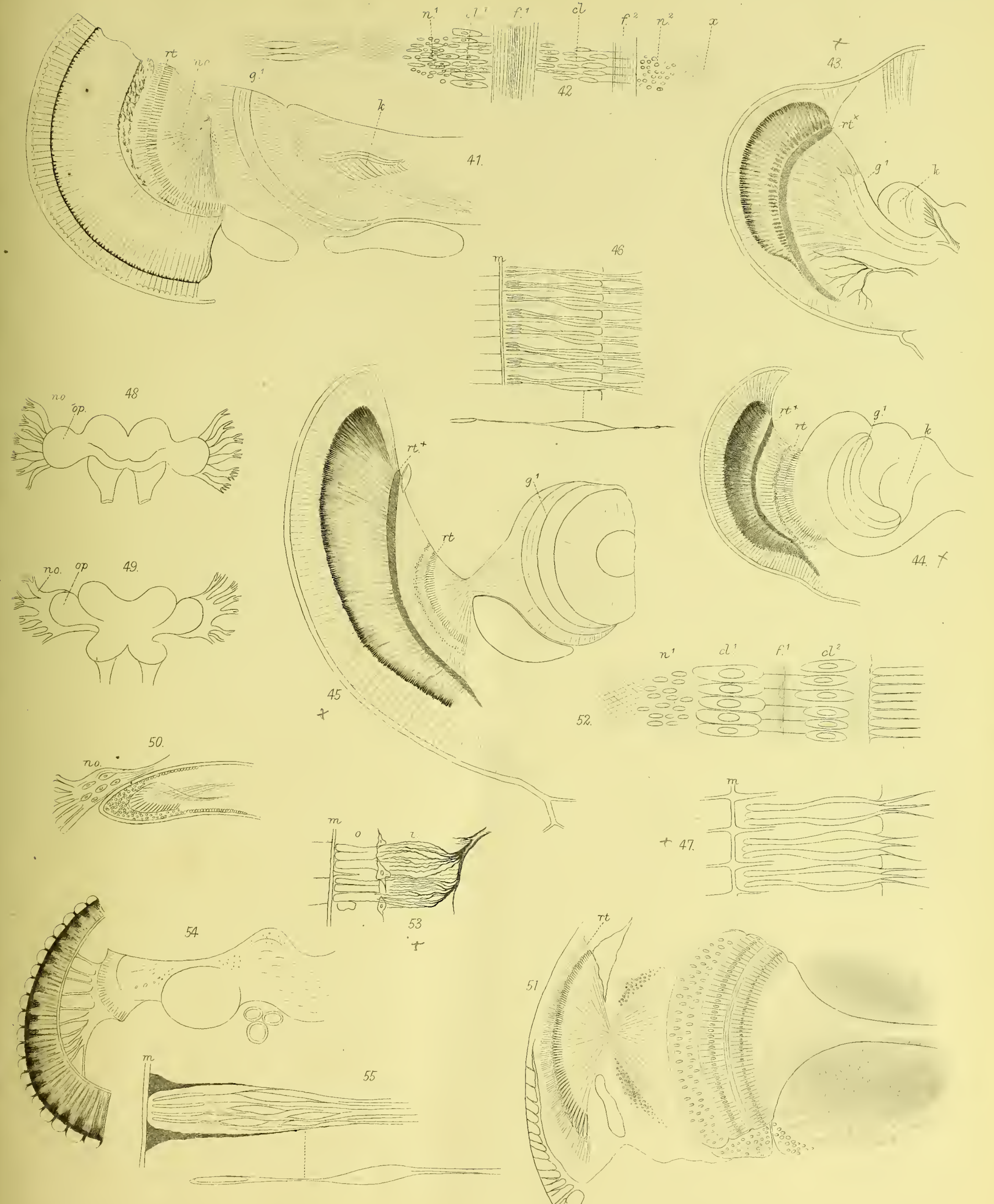

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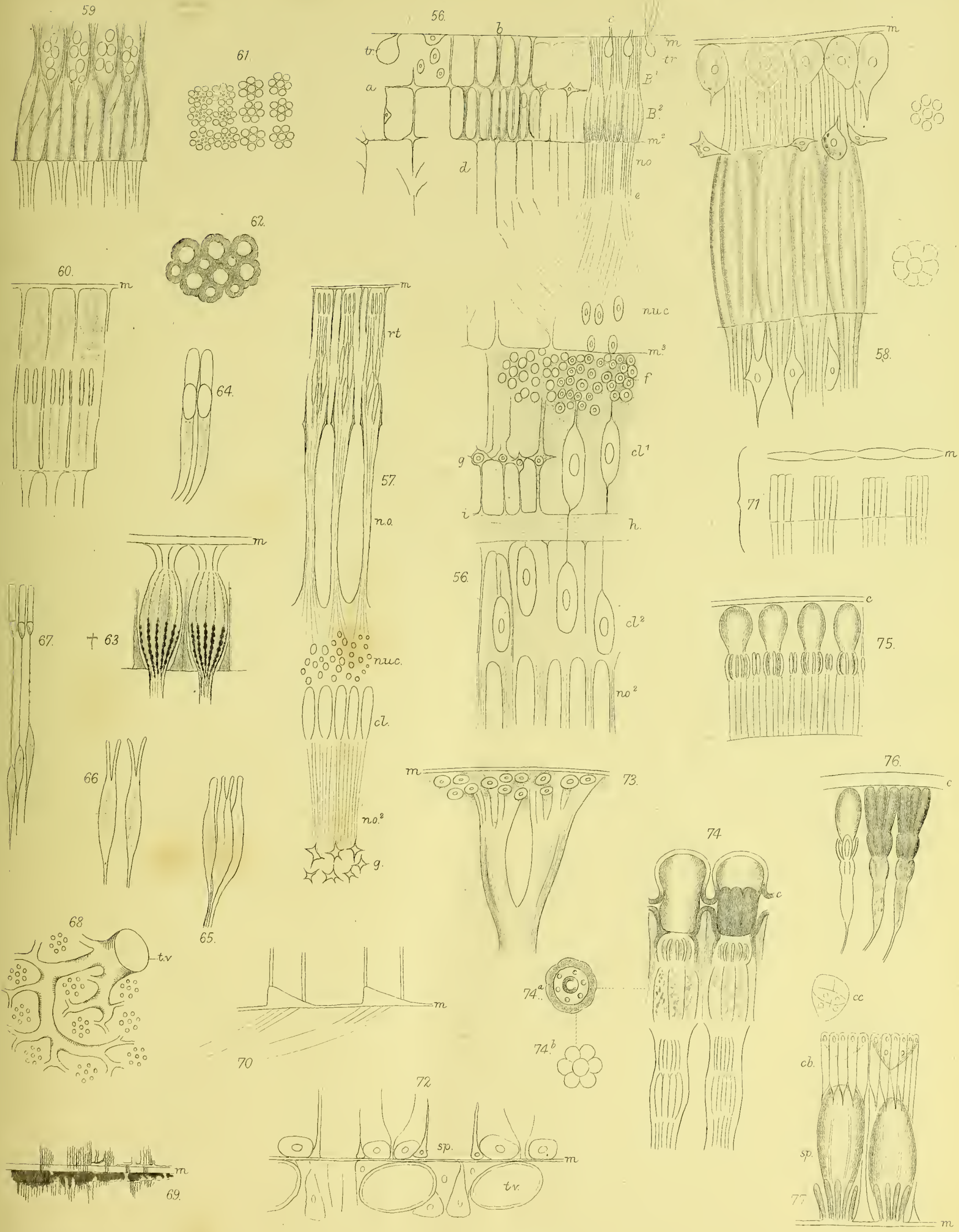

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Part	VI.	1879	1 6 0	0 19 6
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II. Part	I.	1881	0 12 0	0 9 0
Part	II.	1882	0 5 0	0 3 9
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Part	V.	1883	0 3 0	0 2 3
Part	VI.	1884	0 13 6	0 10 0
Part	VII.	1884	0 9 6	0 7 0

H. V. Sebbs
With the author's kind regards

ON THE

MODIFICATIONS

OF THE

SIMPLE AND COMPOUND EYES OF INSECTS.

BY

B. THOMPSON LOWNE, F.R.C.S.,

LECTURER ON PHYSIOLOGY AT THE MIDDLESEX HOSPITAL MEDICAL SCHOOL, ARRIS AND GALE LECTURER ON ANATOMY AND PHYSIOLOGY IN THE ROYAL COLLEGE OF SURGEONS, &c.

From the PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY.—PART II. 1878.

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Suggested

Generalised scheme of arrangement of the Arthropod Eye

1. Cornea divided into a multitude of lenses.

2. Chamber surrounded by pigment, which may contain
a. a! (fasculli) crystal cones, tetrasomes + tetraphores
m. or otherwise modified cells.

3. Rhabdia, surrounded by, or terminating in a second
a." pigment layer, and which may be enlarged
below into fasculli.

4. Limiting Membrane dividing outer Eye from the
m! ganglionic retina.

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ST. MARTIN'S LANE.

5. Stemmata. Only present in certain groups, or replaced
by prolongations of the Rhabdia groupings of
f. r. st. y 36. nerve fibres into bundles. layer of fasculli

6. Nervous Retina. consisting of

a. stellate cells
b. round cells
× c. fusiform cells
d. crossed fibres.

leading to

7. Optic Ganglion. communicating with the Supra Oesop
ganglion.

H. F. Jett
Oct. 1

XVII. *On the Modifications of the Simple and Compound Eyes of Insects.*

By B. Thompson Lowne, *F.R.C.S., Lecturer on Physiology at the Middlesex Hospital Medical School, Arris and Gale Lecturer on Anatomy and Physiology in the Royal College of Surgeons, &c.*

Communicated by Prof. W. H. Flower, *F.R.S.*

Received February 27,—Read March 28, 1878.

[Plates 52–54.]

Although the compound eyes of the Arthropoda have been examined and described with great care in former times by J. Müller,* Leydig,† Gottsche,‡ and Claparede,§ and more recently by Max Schultze|| and Dr. R. Grenacher,¶ the improved methods and instruments of the present time have enabled me to add considerably to the published descriptions of the eyes of insects.

My attention was first directed to this subject by a paper from the pen of Dr. Grenacher. My observations do not accord well with the observations of this author, but I think this is chiefly from the fact that he has used the eyes of immature insects, which differ greatly from those of the mature insect, and from the difficulty there has hitherto been in preparing sections of sufficient thinness to allow the minute structure of the pigmented portion of the eye to be observed. I have been enabled to overcome this difficulty by imbedding the head of the insect in cocoa butter, in the manner first devised by Mr. Schafer, and used by him in the investigation of the early conditions of the mammalian ovum; in this way I have been enabled to obtain sections of the requisite thinness.

In the present communication the principal types of eye are described which I have found in the class Insecta. Reserving the distribution of these types in the class for a future communication, I shall merely indicate the Orders in which each type is found; and in so doing would especially draw attention to the fact that the number of species and genera which I have at present examined is far too small to enable me

* Verg. Phy. der Gesichtssinnes, 1826.

† Müller's Archiv., 1855. Lehrbuch der Histologie, 1857.

‡ Müller's Archiv., 1852.

§ Kol. Zeitsch., band viii.

|| Archiv., band iii., 1867.

¶ Zehender Monatsblatt, 1877.

to state that the eyes described are typical examples of the structure in the Order in question.

I shall conclude with some remarks on the function of the compound eye.

All the preparations, except where the contrary is stated, were prepared from insects hardened in a 2 per cent. solution of chromic acid. I have not found the peroxide of osmium so good in their preparation, and have only used it in a few instances. X

I. *On the Structure of the Stemmata of* Eristalis tenax. (Plate 52, fig. 1.)

I have but little to add to what is already known of the structure of the simple eye. I have at present only examined it in a few of the Diptera, but have found such complete accordance between the descriptions of the authors already named and my observations, that I shall only briefly describe the structure of the ocellus of this insect, as it affords the best starting point for the correct interpretation of the structure of the compound eye.

Fig. 1 represents the ocellus. It consists of a very convex lens, rather more convex on its inner than its outer surface. Immediately behind the lens are the recipient structures, rods (fig. 1, *a*), consisting of an outer and an inner segment. The outer segment (*a*), which is next the lens, is a cylindrical, highly-refractive rod; the inner (*b*) is a fusiform nucleated cell. The inner segments are surrounded and separated from each other by an orange-coloured granular pigment.

The outer segment of each rod is from $\frac{1}{1000}$th to $\frac{1}{500}$th of an inch in length, and $\frac{1}{6000}$th of an inch in diameter; it is finely striated in the longitudinal direction. + These rods are not closely packed together, but seem to lie in a fluid; this may, however, be a *post-mortem* change. Those at the periphery of the eye appear to be twice as long as those at the centre. I have not found them to be doubly refractive, nor have I ever observed any transverse division into disks.

The inner extremity of each rod-cell is connected with a fusiform cell (fig. 1, *c*), or with several fusiform cells arranged one beyond the other, and these are connected with the central nervous ganglion by fine nerve fibres. The fibres are surrounded by a few minute granules of a highly refractive substance. The nerves of the three ocelli unite into a single trunk.

The principal fact to which I would draw special attention is the apposition of the recipient elements of the retina with the lens, and the entire absence of anything like a vitreous body. In the young eye, the percipient structures are separated from the lens by a layer of cells. I have not observed this condition in the present species, but it is seen in the ocellus of the larva of *Dyticus*, *Acilius*, &c.

The great convexity of the lens in the ocellus of *Eristalis* must give it a very short focus, and it is manifestly but ill adapted for the formation of a picture. The comparatively small number of rods must further render the production of anything like a perfect picture, even of very near objects, useless for purposes of vision. I strongly

X Dr Grenacher uses 25% NO_3 to destroy pigment & render his [illegible] transparent - in many cases h[e uses] only alcohol as a hardening agent. My own experience shews me that many of the discrepan[cies] between Dr Grenacher and myself are due to the changes induced by the action of [chromic] acid. The soft parts swell and the hard parts become reduced to mere [illegible] even undergo solution.

+ I regard this as probably the result of optical conditions.

suspect that the function of the ocelli is the perception of the intensity and the direction of light rather than vision in the ordinary acceptation of the term.

II. *On the Structure of the Compound Eye in* Tipula. (Figs. 2 to 5.)

The eye in *Tipula oleracea* is intermediate in structure between a true compound eye and a collection of ocelli.

The curvature of the common cornea is nearly hemispherical. It is divided into a number of strongly convex hexagonal facets, each of which is $\frac{1}{1000}$th of an inch in diameter, and $\frac{1}{2000}$th of an inch in thickness in its thinnest part. The outer surface is more strongly curved than the inner. The axes of the adjacent lenses make an angle of from four to five degrees with each other. Each lens is surrounded by a deeply pigmented portion of the cornea, which forms a black hexagonal framework between the lenses.

Beneath each lens there are sixteen ✗ rod-like cells ⊗ (a''), which are easily distinguished in the immature imago. ⊗ 60 μ in length

In the mature imago these cells are so strongly pigmented with deep black pigment, that even in the thinnest sections I have been unable to detect the divisions between them; neither do they exhibit any transparent openings in transverse sections. I have found this to be the case both in specimens hardened in chromic and osmic acids.

Between each of these opaque cells and the facet of the cornea is a minute highly-refractive globule (a'), of a bright purple colour. These cells bring to mind the highly pigmented retinal cells of the Pigeon.*

Beneath the rod-cell layer is an elongated chamber containing a very remarkable structure, the "retinula" of Dr. GRENACHER, which I shall name the facellus (f). The facellus consists of seven fusiform cells, the outer extremities of which terminate in fine hair-like points, which appear to pass into the rod-like cells of the more superficial layer. The points of the cells of the facellus are the extremities of fine highly-refractive threads, which pass through the fusiform cells of which it is composed, and are prolonged through the long cylindrical organ which connects the facellus with the ganglionic retina. These axial threads are easily distinguished in transverse sections through the facellus (figs. 4 and 4a).

The cells of the facellus appear to become chitinous in the fully-formed imago, and are yellow in specimens hardened in chromic acid; like all the highly-refractive structures of the eye, including the cornea, they resist the action of solutions of caustic alkali for a considerable time. In the immature imago they are slightly granular, especially near their surface, but they contain no pigment.

A strong chitinous membrane (m) separates the parts already described from the

* MAX SCHULTZE, Archiv., bd. iii.

✗ I believe this number is uncertain, and is usually exceeded.

I propose the term Microrhabdia for these rod cells, they are regarded as pigment-cells by Grenacher. Between these cells and the cornea are four cells forming a cone, pseudo cone according to Dr. G. — They certainly ~~exist~~ exist, but were overlooked in my former paper. [that above]. Dr. G. thinks they are the cells of Semper from which the corneal lens is developed — in this I agree — and doubt with him their homology to a true cone —
The fascellus perhaps represents both cone and rhabdome. B. T. Lowne

deeper structures of the eye, but it is perforated beneath each facellus, so that the latter is in continuity with the deeper structures.

A membranous flask-like sac extends from the inner extremity of each facellus to the edge of the corresponding facet of the cornea; this is lined with deep black pigment cells.

Between each facellus and the ganglionic retina is a long compound rod, larger at its outer extremity than at its inner extremity. It is usually spoken of as the rod of the compound eye, but I shall call it the stemon (*st*), as I think I shall be able to show that it cannot be considered as the homologue of the rod-like structure of the true compound eye. ✕

The stemonata, corresponding to the outer facets of the eye (fig. 5), are very short and conical, being very much larger at their outer than at their inner extremities. In the immature imago the stemon can be seen to consist of seven cells, but in the mature insect, and especially in the centre of the eye, these are so perfectly fused together that the component cells of the stemon can be no longer recognised.

The stemon is surrounded at its outer extremity by a very dense sheath of pigment, but this is deficient at its inner end. The stemon contains minute black granules of pigment, and these are arranged in four thread-like lines, which, with comparatively low powers, have an appearance which induced LEYDIG* to describe them as muscular elements; beside these, minute scattered black pigment granules are seen in the protoplasm of the stemon.

Some of the stemonata remain distinct throughout their whole course, but others unite with each other, so that three or four are fused at their inner extremities into a single thread. At their inner extremities all the stemonata branch, and are connected with pigmented stellate cells.

The highly refractive threads of the facellus are seen in transverse sections at the outer end of the stemon, but I have been unable to distinguish them at the inner attenuated extremity.

The stellate cells already alluded to are situated between two fine chitinous membranes. The outer of these (m^1) sends delicate sheaths over the stemonata; the inner (m^2) is perforated by the fine processes of the stellate cells, which communicate with the round cells (g) within the second membrane. The round cells are supported in a fine network of neuroglia, also apparently given off from the inner surface of the second membrane. Beneath the round cells are several layers of fusiform cells (c), which appear to be situated at the outer extremity of the optic nerve, and to be in continuity with its fibres.

III. *On the Compound Eye of* Vespa vulgaris *and* Vespa rufa. (Figs. 7 and 8.)

I have used these two species indiscriminately in the investigation of the compound eye, as I have found no difference in its structure.

* *Loc. cit.*

✕ neither figured nor described by Dr Grenacher – absent in specimens after treatment with liq. Potassa – these appear more like Dr Grenacher's figure.

The type of the compound eye in the Wasp is the same as that of the eye of *Tipula,* but the two differ in the following points :—

The curvature of the general cornea is so slight that the visual axes of adjacent facets in the centre of the cornea only make angles of 8′ with each other. The facets are only $\frac{1}{2000}$th of an inch in diameter, but they are $\frac{1}{1000}$th of an inch in thickness, and consist of numerous layers. The approximate radius of curvature of the outer surface of a facet is $\frac{1}{1500}$th, and that of the inner surface is $\frac{1}{2500}$th of an inch.

The refractive index of the material of which the compound cornea is formed does not differ materially from that of Canada balsam: this is easily seen in specimens mounted in fluid balsam. In order to determine the index of refraction with the greatest accuracy, I found the focal lengths of the lenticular facets of the cornea of a Hornet first in air and then in water, thus eliminating the radii of curvature. By this means I calculated the refractive index to be 1·53. The great difficulty is the determination of the real focus with sufficient accuracy, but the results are sufficiently accurate to give an approximate idea of the position of the focus in the eye. These results give $\frac{1}{200}$th of an inch as the distance of the focus behind the inner surface of the cornea, so that the rays may be considered as approximately parallel to the axes of the rod-cells.

As in *Tipula,* there are sixteen rod-cells (a'') behind each facet. There is also a small highly refractive globule of a dark purple colour, and a facellus (f) very similar to that in the eye of *Tipula* behind the rod-cells. All these structures are surrounded by so much deep violet pigment in my preparations that the details can only be observed with considerable difficulty.

IIIA. *On the Compound Eye of* Formica rufa. (Figs. 6, 7*a*, and 8*a*.)

My description and figures of the eye of this insect are taken from the eye of the mature female imago.

The eye of this Ant differs but little from that of the Wasp. The corneal facets are larger, measuring $\frac{1}{1500}$th of an inch in diameter, but are not more than $\frac{1}{2000}$th of an inch in thickness. The spherules beneath the cornea are colourless. The rod-cells (a'') are imbedded in a large quantity of deep violet pigment (fig. 7*a*) ; they are $\frac{1}{10000}$th of an inch in diameter. The facellus (f) is shorter and wider, and consists of more rod-like cells than I have observed in the facellus of any other insect : there are at least twelve cells ; it is surrounded by a layer of deep purple pigment. The chamber in which the rod-cells lie is lined by deeply pigmented rod-like cells which differ from those in the centre of the chamber in the extent of their pigmentation and in not being connected with the facellus, so that in some of my sections in which the facellus and the deeper parts have been torn away the pigmented rods of the periphery of the chamber alone remain. Under these circumstances the eye appears to be

provided with a chamber like the eye of a true dipterous insect, surrounded with palisade-like rods of pigment. X

The stemon (*st*) is much shorter than that of the Wasp. Each has four elongated cells attached to its surface; these, as well as the stemon itself, are coloured with violet pigment. This pigment is in fine granules, and, like that of the rods in the eye of the Lobster, according to KUHNE,* and that of the eye in all the insects which I have examined, is unaffected by light. The transverse section of the stemonata (fig. 8*a*) shows that they are cylindrical and not prismatic; they exhibit four or more bright spots on their periphery, and are surrounded with granules of purple pigment. I am at a loss to understand the bright spots, but am inclined to view them as the result of molecular change; they may, however, be the indications of highly refractive threads. I have not, however, been able to detect any such threads in the vertical sections.

The stemonata rest on a limiting membrane of chitin (*m*).

I have been more fortunate in the examination of the ganglionic retina of the Ant than in that of the Wasp. The stemon is connected with the nuclear layer by a single thick nerve fibre (*n*); but from what I have seen in the Lepidoptera I have no doubt that by appropriate preparation this would be found to consist of a large number of component fibrillæ. My preparations of the eye of this insect were made from specimens which were killed some two or three years ago by immersion in spirit, and which had been put away and forgotten. The ganglionic retina (*g*) consists exclusively of small nuclei, or perhaps of very small round cells: these are connected with the deeper ganglia by bundles of nerve fibres.

I have not detected any stellate cells, nor have I found the fusiform cells so universally present; but I have not obtained sections of the deeper ganglia; neither have I as yet, in any of the insects which have a semi-compound eye like the Ant, detected the presence of any decussation of the fibres of the optic nerve. I have not, however, obtained a thoroughly satisfactory section of all the parts of the nervous structures connected with the optic tract, owing to the difficulty of getting a section in the plane which includes them all, if such a plane exists, as it certainly does in many of the Diptera and Lepidoptera. I am inclined to believe, however, from what I have seen, that no such decussation occurs in these insects.

IV. *On the Structure of the Compound Eyes of* Eristalis tenax, Syrphus, Musca vomitoria, Stomoxys, *and* Tabanus. (Figs. 9 to 20.)

The eyes of all the Brachycerous Diptera which I have examined are formed on one type, which differs entirely from that on which the eyes hitherto described are formed. They all have a cavity beneath each facet of the cornea containing a slightly coagulable fluid. At the inner extremity of this cavity, which is conical, there is a body consisting of four nuclei or small cells, and beyond this a rod-like structure which apparently differs but little from the stemon. I shall, however, distinguish it

* *Loc. cit.*

X. In the centre of these rods is a true cone of very destructable material. This corresponds with the cone described by Dr. Grenacher in the Bee, and doubtless also exists in the Wasp.

Dr. Grenacher regards the rod cells, Microrhabdia, (mihi) as pigment cells.

The important conditions observed by me in Corethra and the Hive Bee require a de[scription] description which I shall soon furnish — I conclude that the Cone and Lens of Cornea in Insects are inverse in the ratio of their development.

by the term rhabdion, as I think that there is evidence that it does not in any way correspond to the structure which I have named the stemon. I am rather inclined to regard it as the representative of the rod-like cells in the eyes hitherto described. If a fascellus exist at all, it is placed beneath this structure—a fact that is clearly indicated by the position of the fascellus in the eyes of the Lepidoptera, in which there can be no doubt of its presence. As will be seen, there is a structure in the nervous retina of the flies which resembles the fascellus very closely, but a true fascellus is entirely wanting.

Eristalis. (Figs. 9 to 13.)—The eye in *Eristalis* does not differ in any way that I have been able to discover from that of *Syrphus*, but the parts of the latter are often more easily made out from their greater transparency. I shall describe the eye of the former insect, and refer to that of the latter when I have found the parts more distinct in it.

The cornea is about $\frac{1}{1500}$th of an inch in thickness, and the facets average $\frac{1}{800}$th of an inch in diameter. In the centre their adjacent axes make an angle of about 1° with each other. Those in the centre of the cornea are hexagonal and small: usually $\frac{1}{1000}$th of an inch in diameter; those at the edges are square, and as much as $\frac{1}{750}$th of an inch across. The facets in the immature imago and at the periphery of the cornea are surrounded by nuclei of a bright brown tint (the so-called nuclei of SEMPER) (fig. 9 *a*). These appear to be adherent to the substance of the cornea. In the mature imago and in the centre of the cornea the facets are surrounded by a framework of deep black pigment which conceals the nuclei, and is probably developed in or around them. Immediately beneath each corneal facet is a deep cup-like cavity (fig. 9) surrounded by flat cells filled with bright orange-coloured pigment; at the bottom of this cup there are four nucleated cells (a') which rest upon the extremity of a quadrangular rod (figs. 10 *a* and 10 *b*). These parts attain a very high development in *Acridium* and in the Diurnal Lepidoptera. I shall call the four cells the tetrasome, and the quadrangular rod on which they rest the tetraphore.

Between the tetrasome and the nervous retina is the rhabdion (a''). This consists of a protoplasmic sheath, containing a bundle of four fine highly-refractive threads, which are united together at the outer end of the rhabdion into an apparently single axial thread, which enlarges to form the tetraphore. I have been unable to make out the fourfold nature of this structure, but suspect that it consists of four elements. The outer extremity of the rhabdion is cylindrical, and is surrounded by a number of pigment cells (p), forming a structure which has been called the iris. I shall speak of these cells as the outer pigment cells of the rhabdion. In this region the rhabdion is seen to be grooved longitudinally, the grooves being filled by prolongations of the pigment cells (fig. 10 *e*). These details are best seen in sections of the eye of *Syrphus*. Beyond the region of the outer pigment cells the rhabdion is triquetrous, or more rarely quadrangular (figs. 10*f*, and 11); a double bundle of fine moniliform pigmented fibres lies at each angle. These pigmented fibres are partly derived from the outer

pigment cells of the rhabdion, and partly from four pigmented nuclei which are situated at the inner extremity of this structure (fig. 12). These pigmented fibres become very tortuous when they are acted on by water, and apparently produce the contorted conditions of the rhabdion which have been attributed to the elasticity of its axial structure. The interspaces between the prismatic portions of the rhabdia are occupied by large sac-like tracheal tubes. These are, so far as I can tell, confined to the Diptera, and are quite characteristic in this group.

The inner extremities of the rhabdia rest on a strong chitinous membrane (fig. 12, m'), which is perforated for the rhabdia to communicate with the nervous retina beneath, and for the tracheal tubes. The rhabdia appear to be continuous with the thick outer processes of the large stellate cells of the nervous retina (fig. 12). In a few cases I believe I have seen two rhabdia connected with one cell. I have been unable to trace any continuation of the axial structure of the rhabdion into the nerve cells of this region, but in some specimens I have seen four fine processes continued from the rhabdion into the region of the nervous retina, but in these the cells had disappeared in the preparation, so that I cannot state whether these were mere connective elements, or whether they belong to the proper structure of the nervous apparatus.

Fig. 12 shows the inner extremity of the rhabdia and their relation to the nerve structures beneath them. The oval cells are probably embryonic, as I have not found them in the adult imago. The drawing is from the eye of a small species of *Syrphus*, from which I succeeded in getting a very beautiful series of preparations.

The rhabdia of the two peripheral rows of facets are united into bundles at their inner extremities, four or more forming a compound structure, which is surrounded by elongated pigment cells (fig. 10 *l*). These compound rhabdia have six or more pigmented nuclei at their inner extremities. The form of the transverse section of the rhabdia is very variable (fig. 10, *d* to *i*).

The Nervous Retina of Eristalis *and* Syrphus.—As my most successful investigations of the nervous retina have been made in these insects, and as the modifications of the other parts are best understood when the nervous retina is included in the description, I shall describe the nervous retina in these insects, and afterwards state the points in which the same part appears to differ from it in other insects. ✗

Fig. 13 represents this structure. From without inwards there are (g') two layers of ganglion cells, (n) a layer of small round cells, (f') a very remarkable layer of bundles of fusiform cells, so like the cells of the facellus in the eyes of the insects already described that it can hardly be regarded as anything but its physiological representative; and (g'') a third layer of stellate ganglion cells. These structures form the outer ganglionic retina, and are connected by a decussating optic nerve (n') with a still deeper layer of staff-shaped cells, or, rather, with several layers of fusiform cells (c) superimposed one on the other. This inner ganglion is connected with the supracœsophageal ganglion by a distinct peduncle.

The intercommunication of the elements of the external ganglion or ganglionic

E. Berger Untersuch. über de Bau des Gehirns und des Retina der Arthropoden. Wien. 187[illegible]
From numerous observations on the Larva of Libellula, Water Beetle, Crickets, Ants, Bees, Lepidoptera, Artemia, Squilla, Crawfish, &c, states that the following layers are always pr[illegible]
1. Stäbchenschicht, resting on limiting membrane. 2. Nerve bundles. 3. Körner sc[illegible]
4. Molecular schicht. 5. Ganglion ~~F~~ Zellen schicht.
E. Berger's figures are evidently drawn with too low a power, and too little differentiat[illegible]
N.° 2. is certainly not usually present. N.° 3. agrees with my outer nuclear layer. N.° [illegible]
my fusiform cell layer – certainly only molecular when disintegrated. N.° 5. with my in[illegible]

retina is very difficult to determine, but I have no doubt, from the examination of many hundred preparations, that the ganglion cells of the outer layer are continuous with the protoplasm of the rhabdia by their outer processes, and that the stellate cells of the two outer layers form a complex network with each other by their lateral processes. I have been unable to determine whether the inner processes of these cells pass into the small round cells of the third layer, but I suspect they do; they certainly communicate with the fusiform cells of the fourth layer.

Figs. 10, *k*, and 13, *f′*, represent the bundles of cells in this layer. The first is a transverse section through a bundle from a stained specimen. I shall call this the facelloid layer of the retina. The bundles of cells consist of five or six cells. (I am at a loss to explain this deviation from the number of structures in the rhabdion, but it will be remembered that the number of cells in the facellus of *Tipula* is not the same as the number of rod-like elements.)

The innermost or fifth layer of the ganglionic retina (*g″*) is formed of stellate nerve cells like those of the outer layer. These rest on a membrane of extreme tenuity: the inner limiting membrane. This is connected with the outer or basal membrane on which the rhabdia rest by a fine connective network, or neuroglia, in the spaces of which the elements already described are situated. The number of layers of elements is very much reduced in those portions of the retina which correspond to the peripheral portions of the eye. The outer ganglion cells are reduced to a single layer, and the facelloid layer exhibits fewer sets of cells.

The optic nerve (*n′*) consists of clear, often varicose fibres. These unite the inner and outer ganglia, and form a complete decussation from above downwards, as well as from behind forwards. The inner half of each of these fibres is surrounded by a vast number of minute nuclei, which refract light highly. I have been unable to satisfy myself of their connection with the fibres, but I am inclined to the belief that they are united with them, as they move with them when the glass cover is shifted, and are only separated from them with great difficulty. The inner ganglion (*c*) consists of five or six layers of fusiform cells of granular protoplasm.

Musca vomitoria (figs. 14 to 17).—In this insect the chamber of the eye (fig. 14) is shorter than in *Eristalis*, and the tetrasome (*a′*) is placed in a small ovoid cavity at its inner extremity, surrounded by a dense layer of pigment, so that only its apex is exposed to the light. The segments of the tetrasome are finely striated in a longitudinal direction.

The cornea has the curvature of an epicycloid in section (fig. 51, page 596). The facets are $\frac{1}{1000}$th of an inch in diameter; the radius of curvature of the outer surface is $\frac{1}{1000}$th of an inch, and that of the inner surface is $\frac{1}{750}$th of an inch. The focal length of the lens is $\frac{1}{400}$th of an inch, measured in air. The distance of the outer extremity of the tetrasome to the inner surface of the cornea is as nearly as possible $\frac{1}{1000}$th of an inch. The focal length of the lens is given from the same surface of the cornea, so that the tetrasome lies considerably within the focus of the lens.

250 to 100 μ in length. The rhabdia are less regular in size and structure than those of the Syrphidæ, as they intercommunicate with each other in the manner represented in fig. 15. The axial threads vary from four to twelve × after the intercommunication of the rhabdia. The communicating branches contain only two axial threads, and the rhabdia near the tetrasomes contain four axial threads (fig. 15*a*). I do not think the axial threads intercommunicate. Fig. 16 represents the rhabdia and axial threads in transverse section.

Beside the pigmented moniliform fibres of the rhabdia, which are like those in the eye of *Syrphus*, there is a network of stellate pigment cells between the rhabdia, which contain a brilliant rose-coloured pigment; this becomes darker as the age of the insect advances.

A quantity of granular orange-coloured pigment is collected at the inner extremity of each rhabdion in a small spherical mass (fig. 17). The inner extremities of the rhabdia seen *in situ* have the appearance of a layer of polygonal epithelium.

Stomoxys calcitrans.—The only difference that I have been able to observe in the eyes of this insect as compared with those of *Musca vomitoria* is that the corneal facets are smaller: a condition which appertains in all small insects. They are only $\frac{1}{1600}$th of an inch in diameter.

Tabanus bovinus.—I have only examined the eye of *Tabanus* in dried specimens, so that I can only speak of the chitinous framework by which the various parts of the eye are supported. This attains a very remarkable development in *Tabanus* (figs. 18, 19, and 20). Not only are the chambers surrounded by chitinous hexagons, but the rhabdia are invested by chitin, and are connected by membranous septa, which divide the spaces from each other in which the trachea lie. These septa are strengthened by transverse thickenings. The most remarkable deviation from the ordinary structure of the dipterous eye is seen in the structure of the rhabdion, which appears to consist of two separate halves divided from each other by a fissure, each having its own sheath. I have found nothing like this in any other insect; but the structure needs investigation in the recent insect. It is apparently identical with a condition described by Dr. GRENACHER as existing in the rhabdia of some Coleoptera.*

V. *The Structure of the Eye in* Agrion puella. (Figs. 21 to 24).

In *Agrion puella* the type of the eye does not differ greatly from that in the Diptera. The chamber is much deeper and is filled with a gelatinous fluid. It is prismatic in form, and has a ring of four very transparent cells immediately under the cornea (fig. 21*a*); but in *Æschna* there are from eight to twelve cells.† The walls of the chamber (fig. 21) are not surrounded by pigment cells, but sixteen are found around the tetrasome. Long, exceedingly fine processes are given off from

* *Loc. cit.*

† CLAPAREDE. (see note next page)

× Grenacher states that there are always 7 axial threads, other writers like myself give a very variable number. This Dr. G. thinks is not from any difference of structure in different insects, or parts of the eye, but from difficulty of counting. It is due to the fact that the outer third of the rhabdion contains a fasciculus of six rods while four axial threads lie in its interior and extend to the inner extremity of the rhabdion.

these cells which line the chamber. They are moniliform, with small granules of dark brown pigment. The walls of the chamber are chitinous.

The rhabdia are hexagonal in transverse section in their outer extremity (fig. 23, *a*), and in the young imago at least are easily seen to be made up of six cells surrounding the central highly refractive threads. The inner portions of the rhabdia are round in transverse section (fig. 23, *b* and *c*); these organs are everywhere pigmented with fine black pigment. In many of my preparations they contain bright globules like oil; I suspect this is due to degenerative changes during the preparation of the specimens. I have observed the same in the stemonata of *Formica*.

The rhabdia are surrounded by a network of stellate cells containing black pigment (fig. 22).

The trachea of the rhabdia form a network in the spaces between them; but there is nothing like the large blind tracheal sacs found in the same region of the eye in the Diptera.

The external ganglionic retina (fig. 24) differs from that of the Diptera in the large quantity of black pigment developed in it: this is contained in the stellate cells of the neuroglia. The granules or round cells (*n*) are more numerous than in the Diptera, and form several layers, and the place of the facelloid layer of the Dipterous eye is occupied by a triple layer of large prismatic cells (*f* and *n′*). These also contain a large amount of pigment. I have not been able to make out the structures of this portion of the eye with the same clearness as in the Diptera, owing to the pigment in the cells of the neuroglia.

VI. *On the Structure of the Eye in* Acridium (Stenobothrus). (Figs. 25, 26, and 27.)

The cornea is not divided into facets in this insect, but both its surfaces are continuously curved. Beneath the cornea is a framework of chitinous chambers like the cells of a honeycomb; these are $\frac{1}{1000}$th of an inch in diameter. In each chamber there is an exceedingly complex tetrasome; this consists of two parts, which I shall call the tetrasome (*t*) and the tetraphore (*t′*) (figs. 25, 26, and 27).

The tetrasome is placed immediately beneath the cornea. In the young *Acridium*, just before the development of the wings, it consists of four transparent nucleated cells (fig. 25); but in the adult insect these are developed into four spherical highly refractive bodies containing numerous minute vacuoles* (figs. 26 and 27). They are supported on the sides of a square rod-like body formed of four segments, which are enlarged below into the body of the tetraphore. //

The tetraphore in the adult insect consists, like the tetrasome, of a highly refractive substance, probably chitin; but in the immature insect it consists of four cells, which first become chitinous where they are in contact with each other, or they develope a

* Similar vacuoles exist in the tetraphore of *Vanessa*; these have been described by CLAPAREDE, *loc. cit.*

I have here confounded two totally different structures. The four cells from which the cornea is developed, and the remarkable structures which I have since observed and consider as a form of micro rhabdia. There are a great number of these forming a ring immediately beneath the cornea. The outer extremities of the rhabdia are also complete and consist of the united conical highly refractive rods surrounded with pigment, corresponding to the structure marked *a* in fig. 26,

I am inclined to regard this structure as consisting of four highly modified micro rhabdia

rod-like chitinous structure between them, which gradually takes their place. I am entirely inclined to the former view, and regard the segments of this organ as modified cells.

The inner extremity of the tetraphore rests on the outer extremity of the rhabdion, which is swollen into an ovoid enlargement (a). The highly refractive continuation of the tetraphore is plainly seen to be continued as a thread-like process in the axis of the rhabdion (a'). In transverse sections this is easily seen to be composed of four separate fibres. The thread-like axis of the rhabdion is enlarged into two fusiform swellings at the outer extremity of the organ.

The outer extremity of the rhabdion is surrounded by a number of pigment cells; these send fine moniliform pigment threads over it. The pigment is of an olive-brown colour. The rhabdia are cylindrical and straight.

I have at present been unsuccessful in the investigation of the ganglionic retina in this insect.

VII. *On the Structure of the Compound Eye in* Vanessa atalanta. (Figs. 28 to 34.)

The eyes of this insect are similar to the last-described form, but present important differences in the presence of lenticular facets to the cornea, in the structure of the tetraphore, and in the presence of a distinct facellus upon which the rhabdion rests.

The corneal facets are strongly convex on their outer, and slightly concave on their inner, surface; they are $\frac{1}{1000}$th of an inch in diameter.

The tetrasome* consists of four nucleated cells in the immature, and of four highly refractive spheres (t) containing vacuoles in the mature insect. It is placed immediately beneath the cornea. The tetraphore consists of an outer very transparent globe (t''), enclosing an ovoid highly refractive body (t') containing vacuoles. An exceedingly fine prolongation of this body connects it with the rhabdion, and the whole floats in the fluid of the chamber (figs. 28 and 30). The chamber is prismatic, as in the last form; its pigment cells are arranged in two sets: eight surround the edge of the corneal facet, and a second set is situated at the inner extremity of the chamber. Numerous fine moniliform pigmented processes are given off from these cells, those from the outer set interdigitating with those of the inner, and so forming the pigmented lining of the chamber, as in the eye of *Agrion*.

The rhabdia are quadrangular in section, and are of smaller diameter at their outer than at their inner extremities. In transverse section some of these rhabdia appear to consist of five cylinders, but in the majority four of these are fused into a single investing sheath, enclosing an axial structure (fig. 31). Each of the external portions has a pigmented thread, which is easily separated from the rhabdion; it is connected with a pigmented nucleus at its inner extremity.

At the inner extremity of each rhabdion (figs. 32 and 33, a'') there is a cylindrical cavity (a''') formed by a membranous sheath from the basal membrane; the walls of

* four modified microrhabdia.

these cavities are deeply pigmented. Between these cylindrical cavities are others of smaller diameter. Each of the larger cylinders contains seven rod-like cells ; the smaller ones transmit tracheal tubes. I suspect the rod-like cells represent the facelli in the eye of *Vespa* and *Tipula*—a view strengthened by, and indeed entirely resting upon, the condition of the eye in the Crepuscularia. (See fig. 36.)

Immediately beneath the basal membrane there is a grouping together of the nerve-fibres into bundles, which are deeply pigmented with dark brown pigment. Amongst these bundles are a number of large stellate cells (p),* all more or less strongly pigmented, but bearing a very close resemblance to the stellate nerve-cells of the outer ganglion or nervous retina; together with small round and stellate nerve cells (g). Beneath these are numerous elongated fusiform cells (c), arranged in bundles like those of the facelloid layer in the retina of the Diptera, but more nearly resembling the fusiform cells of the deep ganglion of those insects. The fibres of the decussation of the optic nerve, which unite the outer and inner ganglia, are arranged in bundles which have the appearance of large nerve-fibres.

VIII. *On a Modification of the Eye in the Diurnal Lepidoptera.* (Fig. 35.)

The only modification I have observed in the Diurnal Lepidoptera is one in which the tetraphore is placed near the bottom of an elongated chamber; this appears to occur in *Pieris, Colias,* and *Gonepteryx:* the only three genera in which I have examined the eye, except *Vanessa.* Eight very delicate transparent cells (c' and c'') appear to fill this chamber (fig. 35). The lens of the corneal facet has a much less curve on its outer surface in this form of eye. Owing to an accident in the process of preparation, I regret that I am unable to determine from which of these three genera the figure is taken, but they are all very much alike in structure. I believe, however, that it is a drawing from the eye of *Colias.*

Claparede represents a semi-diagrammatic section of the partially developed eye of the pupa of *Vanessa;* it shows the original condition of the chamber of the eye filled with eight cells, in the interior of which the hard structures of the tetrasome are developed. The researches of Claparede on the development of the eye in this genus are very complete, and throw great light on the morphology of the compound eye.†

IX. *On the Structure of the Eye in the Sphingidæ.* (Fig. 36.)

I have not been able to examine the eye in the recent insect, but Prof. Flower placed at my disposal a very fine pupa of a *Sphinx* which had been many years preserved in spirit, from which I obtained some very excellent preparations.

* These cells are figured by Claparede (*loc. cit.*) in a drawing of the parts in the mature pupa. Judging from his figure, they are probably nervous elements.

† *Loc. cit.*

The eye in *Sphinx* is quite intermediate in structure between that of the Nocturnal and of the Diurnal Lepidoptera.

Immediately beneath the cornea, which was still in an undeveloped state in the pupa examined, are four small cells containing nuclei (a'); these rest upon a hard cone, consisting of four segments (a). This structure is characteristic of the eyes of the Nocturnal Lepidoptera, and it is perfectly clear in recent specimens. It persists in the dried insect, like the other chitinous structures. It had assumed an amber colour in the *Sphinx* pupa from which this description is taken (fig. 36, a). Immediately beneath the cone, as I shall call this body, is the rhabdion (a''). This differs in no way from that of *Vanessa*, except in its greater length, and in the fact that its outer end was much contorted. Beneath the rhabdia is a layer of undoubted and true facelli (f): one to each ocellulus. Each facellus consists of seven cells, the slender prolongations of which pass into the corresponding rhabdia. The facelli are surrounded by nucleated pigment cells and are continuous with the nerve-fibres. These are gathered together into bundles and unite into nerve-trunks (st); the fibres from thirty or forty facelli being united into a single trunk. They are deeply pigmented with violet-coloured pigment. At their inner extremity the bundles of nerve-fibres branch, and are connected with stellate nerve-cells. The other structures of the retinal ganglion were not distinguishable. The nerve-fibre bundles appear to represent the stemon of the semi-compound eye of *Vespa* and *Tipula*.

X. *On the Structure of the Eye in the Noctuid Moths.* (Figs. 37 to 42.)

At present I have only examined the eye in the true Noctuids. As in the Crepuscularia, there are four cells (a') immediately beneath the cornea, but in some species these cells each contain one or two bright highly-refractive nuclei, which appear to be formed of the same material as the deeper cone (figs. 38 and 42). The nuclei are rod-like, and have their long axes at right angles to the corneal facet. These cells rest upon a cone (a) formed of four segments, like that in the eye of the Crepuscularia. In some Moths this cone is surrounded by pigment cells which form four lines, one adjacent to each segment of the cone (fig. 38), and give off numerous moniliform fibres, which entirely surround the cone; in other species the cells are reduced to the magnitude of minute granules, from which the pigment fibres of the chamber are given off (fig. 37).

X

The inner extremity of the cone is continued inwards, in the form of four exceedingly fine, highly refractive threads (a''). These are, I believe, always surrounded by a protoplasmic sheath in the recent condition; but in a great many of my preparations the sheath has disappeared, and nothing is left but the highly refractive axial threads. They form the rhabdion. It is not uncommon to find these rhabdia united into bundles which form a network, and in some species the rhabdia are united into complex bundles, which are enclosed in chitinous sheaths surrounded by a large amount of pigment (figs. 39 and 40).

X Add description of details of the cone.

In the eye of the Herald moth (fig. 38) I have found some very remarkable drop-like appendages at the inner extremities of some of the cones (a'''), but I have not been able to make out their nature. I almost suspect they are the result of the rupture of the axial threads of the rhabdion, and are produced by the contraction of these threads, which, if such is the case, are viscous in the recent condition.* The thread-like prolongations of the cone are seen to end at their inner extremities in very long fusiform cells (c), which like the rhabdia are sometimes contained in tubular sheaths of chitin (fig. 41). The inner extremities of the fusiform cells are connected with stellate ganglion cells; but the whole of the deeper structures in the few species I have examined are so deeply pigmented that I am not able to give any satisfactory details concerning the ganglionic retina.

XI. *General Remarks on the Morphology of the Eyes of Insects.*

Three forms of eye have been recognised in the Arthropoda since the time of J. MÜLLER's investigation of the subject: the simple, the aggregate, and the compound eye.

In the simple eye there is no difficulty in recognising the signification of the rod-like elements which are situated beneath the cornea, or their epithelial origin.

There can be little doubt but that we have the highest development of the aggregate eye in the so-called compound eye of the Nematocerous Diptera and of the Hymenoptera.

As far as the cornea is concerned, these eyes do not differ from the true compound eyes of other insects and of many crustaceans; but as I have shown, the deeper parts are similar to those of the simple eye in a high condition of differentiation. This form of eye is therefore to be regarded as a highly developed form of a connecting link between the simple and compound eye.

I am at present unable to point out in a satisfactory manner the nature and morphological relations of the facellus. Although this structure is present in the eyes of many Lepidoptera, it is apparently absent in the true Diptera, unless the facelloid layer of the retina can be regarded as its representative. The morphological representative of the facellus is more probably found in the pigmented bundles at the inner extremity of the compound rhabdia of the periphery of the eye in these insects.

A comparison of the parts in the aggregate eyes of the Nematocerous Diptera and Hymenoptera with the structures in the true compound eye is not difficult, but it can only be made in a tentative manner until the development of the aggregate eye has been more thoroughly worked out and a comparison has been made with the

* A similar contraction has been observed by MAX SCHULTZE in the inner extremities of the rods of Vertebrates, as a *post-mortem* condition. (Archiv., band iii., p. 220.)

development of the compound eye: a task which I shall hope to commence at least next summer.

CLAPAREDE'S paper, which is most accurate, gives very valuable details on the development of the true compound eye.* He has also described and figured the various stages of the development of the eye of *Formica*, but he has neither detected the rod-cells of the chamber nor the facellus: I cannot help thinking that this has been from the manner in which the stemon separates from the fasel~~ce~~llus. I strongly suspect that CLAPAREDE'S preparations represent only a part of the eye, and that in the more advanced stage the chamber is only partially represented. Unless this is the case, the remarkable deviation in the Hymenoptera from the more usual form of the eye in insects is developed from an eye which differs in no important particular from the compound eye in its simplest condition.

The true compound eye of insects is seen in three very different forms in the fully developed insect; but the observations of CLAPAREDE show that in the undeveloped condition of the eye these are all most probably identical, or nearly so. In this condition each segment of the eye consists of thirteen principal cells: eight form the cone (Krystalkegel) and five represent the rhabdion. Beside these there is a variable number of pigment cells. #

The highly refractive structures of the axis of these parts are probably formed by the deposit of chitin in the substance of the primitive cells; but I think that further investigation of the whole subject is needed. Although my observations on the development of the compound eye agree in the main with those of CLAPAREDE, I have yet to work out the subject with the increased knowledge which I now possess.

The view that the hard and highly refractive parts of the cone or chamber are formed in the interior of the primitive cells is borne out, however, by the condition of the cone in the Nocturnal and Crepuscularian Lepidoptera, and according to LEYDIG† in the eye of *Cantharis melanura, Elater noctiluca,* and *Hyperia,* where the whole of the large cells of the primitive cone are replaced by the hard scleral cone.

I shall call the form of eye typical of the Nocturnal Lepidoptera the conic eye: and shall speak of the conic eye as proto-conic in its embryonic condition, and sclero-conic in the form it assumes in the Nocturnal Lepidoptera, and many other insects.

At present I have not found the proto-conic form of eye in any fully developed insect, but I have not yet examined the eyes of the Coleoptera, in which the writings of previous observers render it highly probable that such eyes exist, at least amongst the Pentamera. The work of LEYDIG shows that it exists in Melolontha.

Starting from the conic eye as the nearest approach to the primitive eye, there are two very remarkable and opposite deviations. In one, the cone is replaced by fluid, and the recipient structures are reduced to their simplest condition, as in the eyes

* *Loc. cit.*

† *Loc. cit.*

Claparede's work is evidently right in every particular – my difficulties have all been removed by the discovery of a true cone in the eyes of the Hymenoptera – The development of both cone and microrhabdia has been accurately made out by Claparede – The view I think most probable now is that just as there are rods & cones in the vertebrate eye there are rhabdia and microrhabdia in those of arthropods – their relative functions are still unknown.

of the Brachycerous Diptera, and the Dragon-flies. I shall speak of this as the hydro-conic eye.

In the other form the cone is highly modified, and appears as a very complex tetrasome and tetraphore. I shall speak of this as the tetraphoric eye.

I shall conclude this portion of the subject by indicating very briefly the probable distribution of the three forms of compound eye, as well as that of the highly complex semi-compound eye, which for brevity may be called micro-rhabdic.

I have at present found the micro-rhabdic eye in the Nematocerous Diptera, the Hymenoptera, and Hemiptera, although I have only examined the eyes of a few members of the Order, and these far from exhaustively. I believe that it will also be found in the eyes of many Coleoptera, such for instance as Bryaxis.

The conic eye is the usual form of the compound eye in the Crustacea: at least it is found in the Lobster, Palæmon, and Hyperia. As already stated, it is found in the Nocturnal Lepidoptera, in the Sphingidæ, and probably in all the Pentamerous Coleoptera at least.

Judging from Leydig's descriptions, it is also found in the Cursorial Orthoptera.

I have at present found the tetraphoric eye only in *Vanessa, Colias, Pieris, Gonepteryx,* and *Acridium;* but I have not examined any other species of the Orthoptera and Diurnal Lepidoptera. The hydroconic eye occurs in all the Brachycerous Diptera and in the Dragon-flies.

XII. *On the Theory of Mosaic Vision.*

The structure of the compound eye appears to favour the view long ago expounded by Joh. Müller. This view is supported by the absence of lenticular facets in many species of Arthropods; by the relative sharpness of vision, not only in different species, but in different parts of the field of the same eye, as well as by the behaviour of a beam of light in passing through a highly refractive rod immersed in a less highly refractive medium, or surrounded by black pigment.

It is, further, the only theory which has been hitherto advanced that is competent to explain the phenomena when we bear in mind the relation of the recipient structures of the compound eye to the nerve elements beneath them.

On the passage of a ray of light through a highly refractive rod of small dimensions.—In order to arrive at some knowledge of the manner in which light passes through the highly refractive rods of the eye in the Arthropoda, I made the following experiments.

I took a capillary glass tube about $\frac{1}{100}$th of an inch in diameter, and placed it upright in a small transparent trough under the microscope, and filled both the vessel and the tube with water. The tube was an inch in length and was examined with an inch objective. I found that no light passed through the lumen of the tube, but that the section of the wall of the tube was brilliantly illuminated. I next placed a few fine

X. In the eyes of Dragonflies Microrhabdia are present.

O A great difficulty arises from the Opthalmoscopic appearance of the fundus of the Eye.

The Cone is developed inversely with the lenticular structure of the Cornea.

The Basillus of the Nematocerous Diptera perhaps consists of a Cone and microrhabdia. The base of the tetraphore appears to be a Cone & the Eye is conic, and remarkably modified in Corethra.

glass threads, drawn from glass rod, in the interior of the capillary tube; these were as nearly as possible the same length as the tube, and measured $\frac{1}{1000}$ of an inch in diameter. The end of each of these fine rods appeared as a small bright disk in the deep black lumen of the tube, and when the light was shut off from the rest of the field reminded me of the appearance of the disk of a planet seen through a telescope, although the illumination was not by any means powerful, but was obtained from an ordinary gas burner ten feet from the microscope. When the focus of the microscope was altered so that the ends of the rods lay beyond it, the circles of light enlarged, showing that the rays left the rod in a divergent direction.

The same phenomena were observed when the diameter of both the rods and the containing tube was somewhat increased, but they were not so brilliant. In some cases when the ends of the rods were beyond the focus of the object glass, the central spot of light was surrounded by grey rings from interference. When the extremities of the rods were lenticular, as well as when the lower end of the rod was enlarged by fusing it into a globule of glass, or when it was drawn into a cone, the same phenomena occurred; so the brilliancy of the upper extremity of the rods was increased when the light, falling on the lower extremity, was convergent, so long as the axis of the ray was in the same direction as the axis of the rod, although oblique pencils produced only very feeble illumination of the upper extremity of the rod, even when the obliquity was only slight—at most, three or four degrees from the axis of the rod.*

It appears pretty evident that the appearances described are due in some way to total internal reflection.

In order to estimate the effect of the pigment I used glass rods, covered, except at their ends, with a layer of black varnish; and I found that even with rods $\frac{1}{500}$th of an inch in diameter, and only half an inch long, it was very difficult to transmit any light at all, unless the rays were absolutely parallel with the axis of the rod. With longer lengths of rod, or rods of smaller diameter, no light was transmitted, and the ends of the rods appeared quite black.

From these facts I think the inner extremities of the fine rod-like structures of highly refractive material which extend from the cornea, or from the inner end of the chamber into the deeper structures of the eye, may be regarded in the light of luminous points, illuminated by the light of the central pencil transmitted through the lens, and having as their function the excitation of the nerve ending in which they are embedded.

The focus of the lenticular facet in all the insects which I have examined lies considerably deeper than the outer extremity of the rhabdion in the true compound eye, and much below the surface of the rod-like recipient structures in the micro-rhabdic eye, so that for objects removed only the tenth of an inch or less from the

* OSCAR SCHMIDT has since recorded some similar experiments with glass rods in KÖLLIKER, 'Zeitsch. für Wissensch. Zoo.', Bd. 30. Beiblatt.

facet, we have to do with convergent rays and not with the focal point. This points to some mode by which the stimulation of the nerve ending is brought about, other than the union of homocentric pencils in a point beneath the compound cornea. In *Hydrophilus piceus*, however, according to EXNER,* the focal point for parallel rays lies within the crystal cone.

Whether each facet in the compound eye corresponds to one or to four distinct luminous impressions must at present, at least, remain a matter of doubt. I think, however, there can be no doubt that several distinct luminous impressions are transmitted from each facet in the micro-rhabdic eye of *Tipula* and *Vespa;* and there can be no doubt that a number of distinct luminous impressions are received by the ocellus or simple eye. I cannot, however, believe that the ocelli of insects can produce anything worthy of the name of an image, in the Diptera and Hymenoptera at least. The few retinal elements, their near approach to the lens, and the strong curves of the surfaces of the latter, are but ill adapted for more than the perception of light and the direction in which it is most intense.

In the compound eye the curvature of the cornea and the number of facets agree well with MÜLLER'S theory. It is true that CLAPAREDE has expressed the opposite opinion, but I think I shall be able to show that this is based on an incorrect assumption.

CLAPAREDE has stated that if MÜLLER'S theory were true, a hive Bee should be unable to perceive objects of less than eight or nine inches in diameter at a distance of 20 feet as distinct; but he comes to this conclusion by assuming that the acuity of vision is the same over the entire field. This is far from being the case in any insect which I have examined, with the single exception of *Tipula*, where it is approximately so, perhaps. In all the other insects which I have examined, the axes of vision for adjacent facets make a very small angle with each other in the central portion of the visual field, and a much larger one at its circumference. And although I have not had the opportunity of examining the cornea of the hive Bee critically, in the humble Bee, the Wasp, Tabanus, and the great Dragon-flies, the angles made by the axes of adjacent facets are not more than from eight to fifteen minutes: a condition which would enable objects of from half an inch to an inch in diameter to be seen as distinct at a distance of twenty feet—an acuity of vision quite sufficient to account for all the observed phenomena of vision in insects.

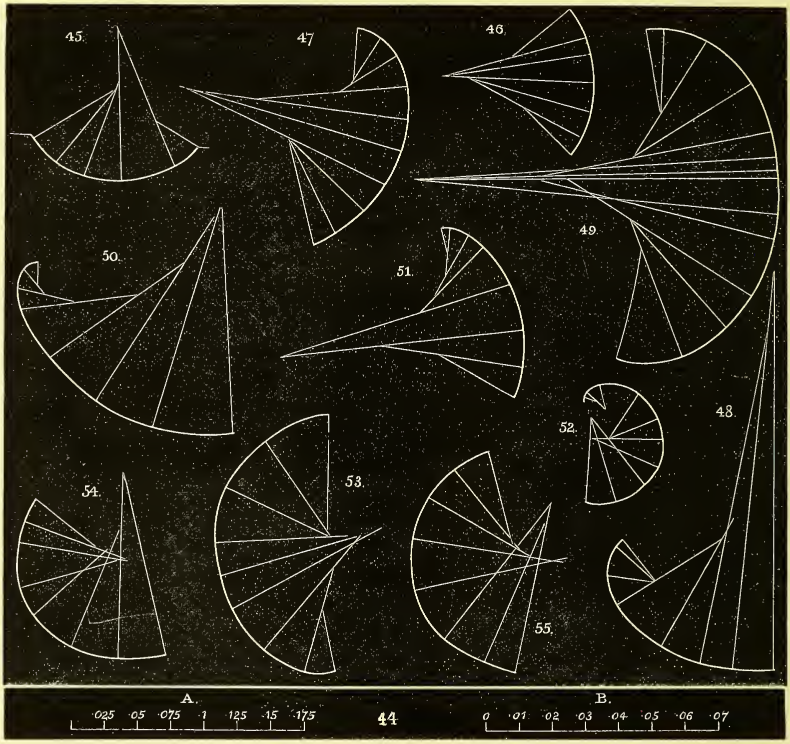
The method which I have adopted in calculating the acuity of vision is as follows:—

A magnified image of the entire cornea is thrown upon a sheet of paper by means of a camera lucida attached to the microscope. By using low powers and appropriate illumination, the error from distortion of the image can be reduced to a minimum. The profile of the various meridians was then sketched. By drawing tangents to the curve, the radii of curvature of different parts of the curve are readily found. The ratio of the diameter of the facets to these radii gives the sine of the angle subtended

* Wien Sitzungsberichte, 1876.

by each facet. It will be seen by the accompanying figures (figs. 45 to 55)* that the curves of the meridians of the compound cornea approach more or less closely to an epicycloid.

The average angles subtended by the facets in the region of most distinct vision in different insects are given in the following table, in which I have added the greatest angles subtended by the facets at the periphery, the diameter of the corneal facets and



the acuity of vision, both in the centre and at the periphery; according to SNELLEN'S system, the unit of vision being the power of perceiving an object at twenty feet, which has a diameter corresponding to an angle of five minutes: an angle of one minute being taken as the mean size of a visual perception in man. The signification of the fraction in the fourth and fifth columns is, that an object appears in the same detail to the insect as it does to man, when the distance of the object from the eye is

* See description of plates, p. 602.

measured by the denominator of fraction for man, and by the numerator for the insect. Thus a Dragon-fly would see an object 20 feet from its eye in the same detail that a man would perceive if it were seen at a distance of 160 feet.

	Least angle.	Greatest angle.	Diameter of facets.	Greatest sharpness of vision.	Least sharpness of vision.
Æschna grandis	8′	30′	$\frac{1}{750}$	$\frac{20}{160}$	$\frac{20}{600}$
Vespa rufa, worker	8′	85′	$\frac{1}{2000}$	$\frac{20}{160}$	$\frac{20}{1700}$
„ *vulgaris*, worker	8′	85′	$\frac{1}{2000}$	$\frac{20}{160}$	$\frac{20}{1700}$
Bombus muscorum, female..	8′	30′	$\frac{1}{1000}$	$\frac{20}{160}$	$\frac{20}{600}$
Tabanus bovinus, male	18′	12°	$\frac{1}{1000}$	$\frac{20}{360}$	$\frac{20}{14400}$
Syrphus, sp.	1°	4°	$\frac{1}{1000}$	$\frac{20}{1200}$	$\frac{20}{4800}$
Musca vomitoria	1°	6°	$\frac{1}{1000}$	$\frac{20}{1200}$	$\frac{20}{7200}$
Colias edusa..	1°	2°	$\frac{1}{1000}$	$\frac{20}{1200}$	$\frac{20}{2400}$
Noctua, sp.	2°	12°	$\frac{1}{1000}$	$\frac{20}{2400}$	$\frac{20}{14400}$
Tipula oleracea	4°	5°	$\frac{1}{1000}$	$\frac{20}{4800}$	$\frac{20}{6000}$

The region of the most distinct vision extends from the visual line or the perpendicular to the centre of the least curved portion of the cornea, to a distance of from twelve to fifteen degrees in the horizontal, and from twenty to thirty degrees in the vertical meridian; so that the region of the most distinct vision for each eye is approximately half an ellipse, with its long axis vertical in front. But when the two eyes are taken it is approximately a circle in front of the insect; the two fields do not overlap in this direction.

It will be seen that the acuity of vision, according to MÜLLER's theory, must vary directly with the radius of curvature of the surface of the cornea, and inversely as the diameter of the corneal facets. In many of the Diptera, as in *Tabanus*, the facets of the peripheral region of the cornea are three times the diameter of those in its centre.*

The size of the corneal facets varies in different insects from $\frac{1}{750}$th to $\frac{1}{2000}$th of an inch. They seem to bear a relation to the size of the insect, as the largest are found in the largest and the smallest in the smallest insects; but I have found none less than $\frac{1}{2000}$th of an inch, although I have examined the eyes of many Diptera, of a line or less in length. As the radii of curvature in very small insects are also very short, the vision of such insects is less distinct than that of larger insects; at least, the distance at which objects can be seen distinctly must be very small.

J. MÜLLER has pointed out that the flight of insects depends on their power of vision, and this will account for the distances which large insects sweep through when

* In the genus *Æschna* the facets of the upper third of the compound cornea are twice the diameter of those of the lower two-thirds; there is apparently no difference in the other part of the eye, except a proportionate increase in size.

disturbed, whilst the smaller species are confined, as a rule at least, to short flights, and remain hovering around a single branch or twig, unless carried away by currents of air.

The direction of the visual line is also a point of considerable importance. The fields of most acute vision are so combined in *Tabanus* that the visual line is directed forwards in the horizontal plane of the insect. In the pollen-feeding Diptera, and in most Lepidoptera, the visual lines diverge from each other to the extent of from fifteen to thirty degrees, and are directed downwards at an angle of thirty degrees, instead of lying in the horizontal plane.

In the Wasp the line of vision is directed forwards; in a species of *Noctua* it is directed almost directly downwards; and in the great Dragon-flies, where a very large field exists in which the visual power must be very great, the visual lines are directed forwards in the plane of the insect, diverging from each other to the extent of about thirty degrees.

In all the Coleoptera which I have examined, although the corneal facets are small, the radii of curvature of the cornea are very short; so that they cannot see objects distinctly in detail at any great distance. The same is true of the ants.

J. MÜLLER has stated that the vision will be the same for distant as for near objects, and this is true if measured by the angle under which the smallest object is seen as a distinct visual impression; but it will make a great difference in the details which can be perceived whether the object, as for instance another insect, subtends an angle of only one degree, or of from fifty to sixty degrees. By means of the fourth column in the table given above we may also estimate the distinctness with which near objects are seen by the species of insects in question. I have often been struck with the fact that the mimicry of the Diptera to the Hymenoptera is only sufficiently close when the insects are seen at a distance to be likely to afford any protection to the Diptera; but if the view of MÜLLER is the true one, and the acuity of vision is expressed in the above table, it would be sufficiently close to deceive the majority of other insects even at close quarters. I have frequently observed that Flies give place to both Wasps and the Syrphidæ which resemble them.

Under the supposition that MÜLLER's theory is the true one, I was for a long time much puzzled to account for the lenticular facets of the cornea. That they are not essential to the vision of insects is apparent from the frequent absence of such facets both in insects and crustaceans, which give the strongest evidence of very considerable acuity of vision. My experiments, however, with glass rods seem to point to the explanation that these facets enable a larger pencil of rays to reach the inner extremity of the highly refractive parts of the eye; for instance, when a cone exists, the axial cone of light entering the rhabdion will be much larger with a lenticular facet than when no lens exists.

There are some very interesting facts with regard to the distribution of lenticular facets in the Insecta. Thus some Noctuids have practically no lenticular facet, or, at

least, a very feeble one, whilst others have a very convex lens. The same is true in the Diurnal Lepidoptera. In Hydrometra the corneal facets are composed of two parts of different refractive powers. The outer portion of the cornea is more strongly refractive than the inner portion; it is also more convex on its inner surface than the inner surface of the corneal facet, so that it presents the condition of a very powerful bi-convex lens in apposition with a second lens, which is concavo-convex, the two fitted together like an achromatic object glass. In *Dyticus* there is also a remarkable arrangement: the corneal facets have a scleral cone adherent to their inner surfaces. I have at present examined only dried specimens, but hope to continue the investigation.

The region of binocular vision.—In most insects the field of vision in the two eyes has a common portion in the peripheral region in the vicinity of the mouth; in this region the radius of curvature of the cornea is very short. It is, therefore, only adapted for the acute vision of very near objects. It is chiefly developed in predaceous insects. It probably serves the insect in judging of the distance of objects from the mouth.

J. Müller, in his classical work 'On the Comparative Physiology of Vision,' states that no portion of the compound eye in any of the insects he examined corresponded in the direction of the axis of the facets with the eye of the opposite side; but he does not appear to have examined the eyes with sufficient minuteness to have been able to detect the slight overlapping of the two fields which I have described.

Description of the Plates.

PLATE 52.

Fig. 1. The ocellus of *Eristalis*.

Fig. 1*a*. One of the rod cells of the same.

Fig. 2. A vertical section of a portion of the compound eye of the common Crane-fly.

Fig. 3. A vertical section of a portion of the chamber of the compound eye of an immature Crane-fly, showing the rod cells and the facellus.

Fig. 3*a*. One of the facets of the same eye seen from without, showing the extremities of the rod cells beneath.

Fig. 4. A transverse section through the middle of the facellus.

Fig. 4*a*. A section through the lower extremity of the facellus.

Fig. 5. The stemon and nervous retina of the same.

Fig. 6. A vertical section of a portion of the compound eye of the female of *Formica rufa* (from a specimen preserved in spirit).

Fig. 7. The rod cells, facellus, and stemon of the eye of the Wasp.

Fig. 7*a*. A transverse section immediately below the cornea of the eye of *Formica rufa*.

Fig. 8. Transverse section through the rod cells of the eye of the Wasp.

Fig. 8*a*. A transverse section through the stemonata of the eye of *F. rufa*.

(Figs. 9 to 13, inclusive, are in Plate 53.)

Fig. 14. The chamber from the eye of the Blowfly.

Fig. 15. The rhabdia of the same.

Fig. 15*a*. A portion of one of the rhabdia of the same.

Fig. 16. Transverse sections through the rhabdia of the same.

a and *b*. Compound rhabdia.

c and *d*. Simple rhabdia.

Fig. 17. The inner extremities of the rhabdia and the nuclear masses of pigment seen from the retinal surface of the rhabdia.

Fig. 18. The rhabdia and chambers of *Tabanus*, from a dried insect.

Fig. 19. A portion of two rhabdia from the same.

Fig. 20. The chambers of the eye of *Tabanus*.

The details in all the figures are drawn with a Nachet $\frac{1}{16}$th immersion.

PLATE 53.

Fig. 9. Section through one of the elements of the compound eye of *Eristalis*.

Fig. 9*a*. Four facets of the cornea, showing SEMPER's nuclei.

Fig. 10. Details of the compound eye of *Eristalis*.

a. Transverse section through the tetrasome.

b. Transverse section immediately below the tetrasome.

c. Section through the lower end of one of the rhabdia from near the periphery of the eye.

d. Section just above the pigment cells of the rhabdion.

e. Section just below the pigment cells.

f, *g*, and *i*. Sections through the rhabdia.

h. Lower end of one of the rhabdia, with six pigmented nuclei from near the periphery of the eye.

k. Section through a facellus from the facelloid layer of the retina.

l. Lower end of a compound rhabdion from near the outer edge of the eye.

Fig. 11. A portion of one of the triquetrous rhabdia.

Fig. 12. Lower end of the rhabdia to show their connexion with the nervous retina.

Fig. 13. The nervous retina of *Eristalis*.

Fig. 21. Two chambers from the eye of *Agrion virgo*.

Fig. 21*a*. Four facets from the same eye seen from the outer surface.

Fig. 22. A portion of one of the rhabdia.

Fig. 23. Transverse sections of the rhabdia.

a. Section throughout the outer extremity of a rhabdion.

b and *c.* Through the middle of the rhabdion.

Fig. 24. The ganglionic retina of the same insect.

(For figs. 25, 26, and 28, see Plate 54.)

Fig. 27. The tetrasome of *Acridium* seen from the surface of the cornea.

Fig. 29. The tetrasome of *Vanessa atalanta.*

PLATE 54.

Fig. 25. The chamber of the eye of the nymph of *Acridium.*

Fig. 26. The same, from an imago of the same.

Fig. 28. Two chambers from the eye of *Vanessa atalanta.*

Fig. 30. Four chambers seen from the surface of the cornea. For the sake of clearness, all the parts are only represented in one of the segments.

Fig. 31. The rhabdion of the same.

Fig. 32. Transverse section through some of the facelli of the same eye.

Fig. 33. The ganglionic retina.

Fig. 34. Vertical section through one of the facelli of the same eye.

Fig. 35. The chamber of the eye of *Colias.* cf. Pro. [illegible] 645

Fig. 36. A vertical section of a portion of the eye of a Hawk Moth from the pupa.

Fig. 36*a.* One of the cones of the same.

Fig. 37. One of the cones of the compound eye of a Noctuid.

Fig. 38. A vertical section of a portion of the eye of another species of Noctuid.

Fig. 39. A similar portion of the eye of a third species of Noctuid.

Fig. 40. A transverse section through the compound part of the rhabdion, from the same insect as the last preparation.

Fig. 41. A transverse section through sheaths of the rhabdia of a Noctuid Moth.

Fig. 42. The cones seen from the cornea, from the same specimen as fig. 38.

Fig. 43. An outline of the eye of *Vespa* to show the direction in which the principal meridians were drawn.

DIAGRAM. (Page 596.)

Fig. 44. Scales of fractions of an inch to which the succeeding diagrams are drawn.

(For figs. 44 to 54, see page 596.)

Fig. 45. The principal horizontal section of the cornea of *Vespa* (scale A).

Fig. 46. The vertical meridian of the same eye (scale A).

Fig. 47. The curvature of the principal vertical meridian of a species of *Syrphus* (scale B).

Fig. 48. The curvature of the principal horizontal meridian of *Æschna grandis* (scale A).

Fig. 49. The principal vertical meridian of the same (scale A).

Fig. 50. The horizontal meridian of *Tabanus bovinus* (scale A).

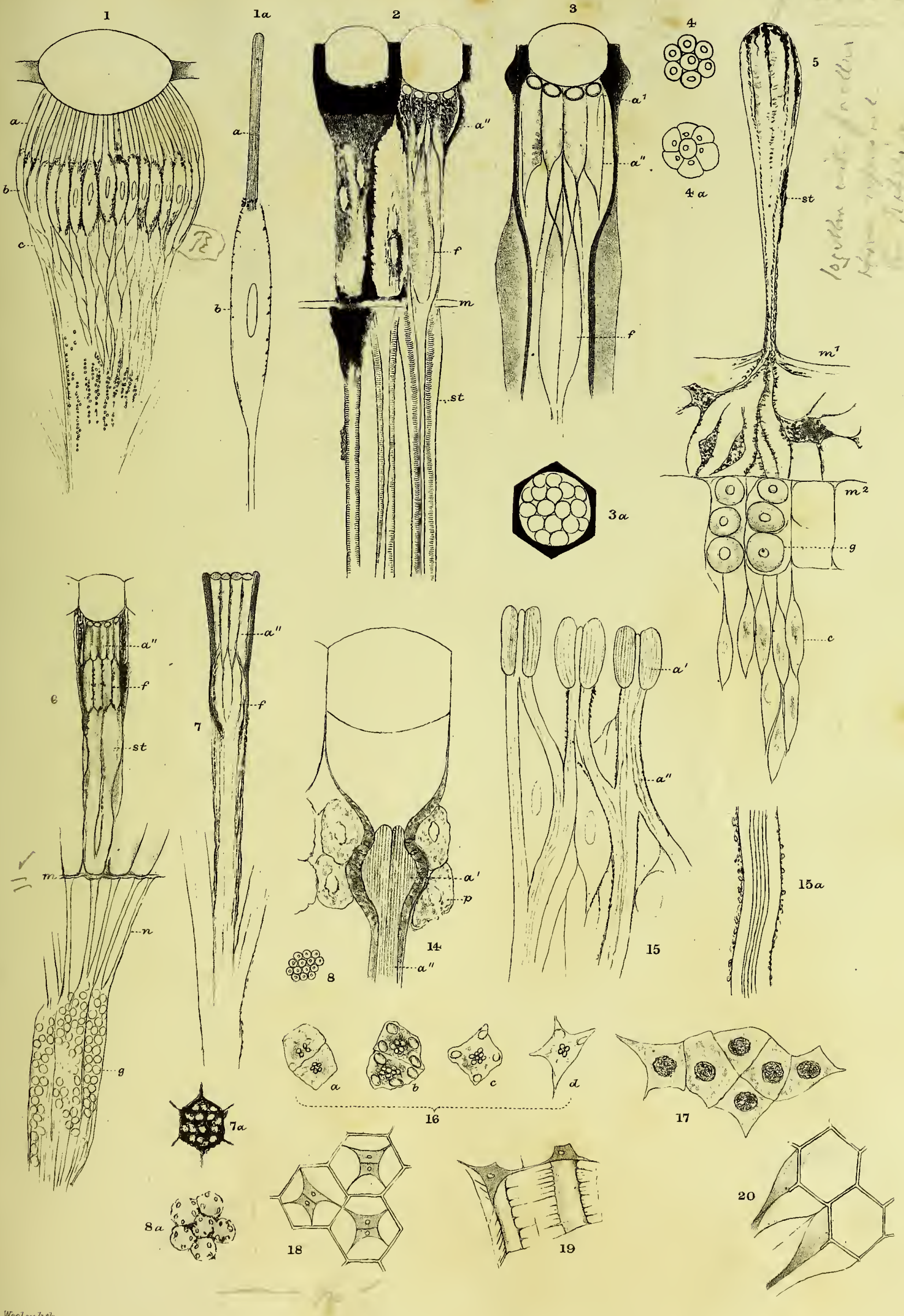
Fig. 51. The principal vertical meridian of *Musca vomitoria* (scale B).

Fig. 52. The vertical meridian of the eye of a Noctuid Moth (scale B).

Fig. 53. The principal vertical meridian of the eye of *Colias edusa* (scale B).

Fig. 54. The same, a meridian 30° from the last (scale B).

Fig. 55. The same, a meridian at right angles to the last (scale B).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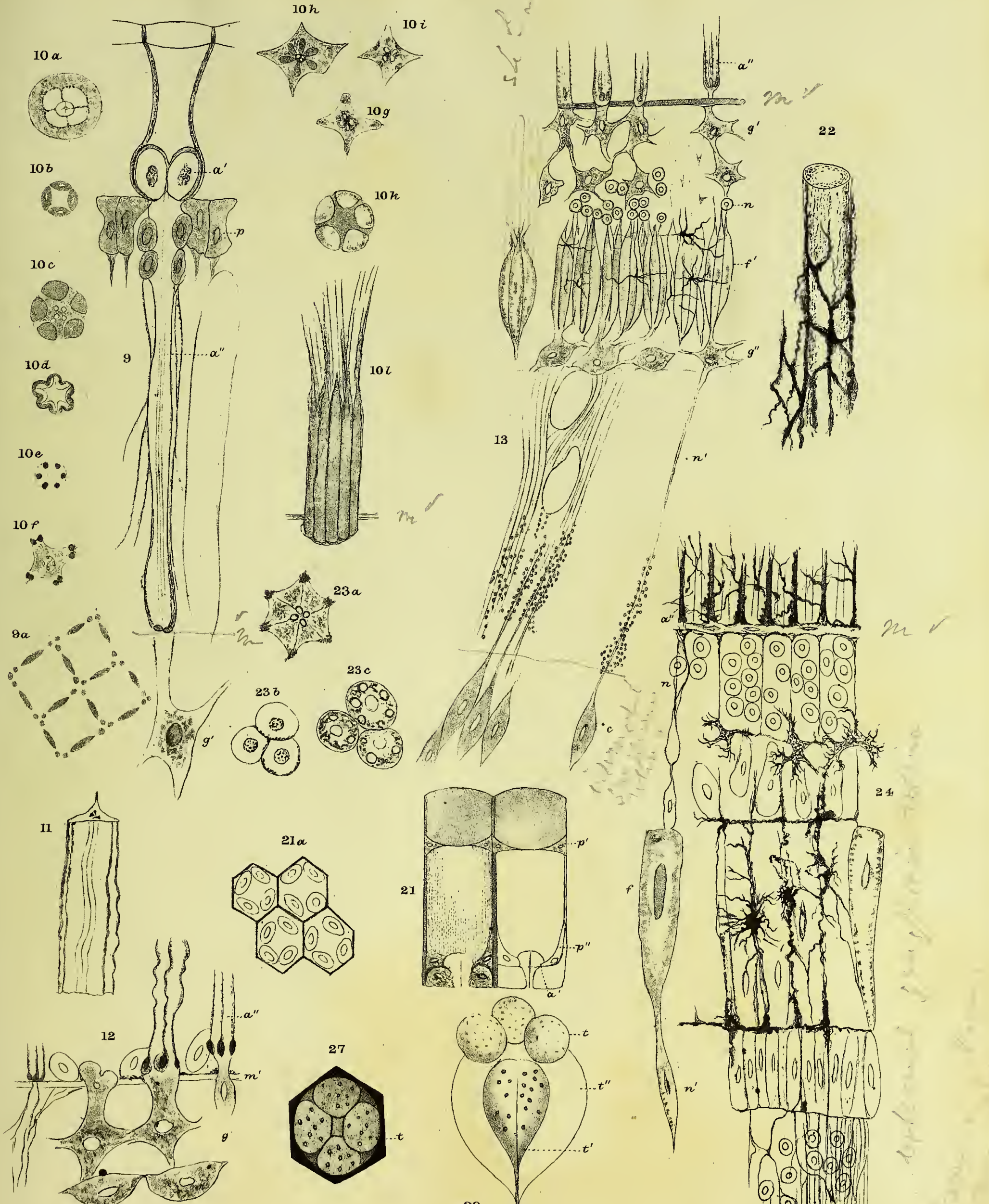

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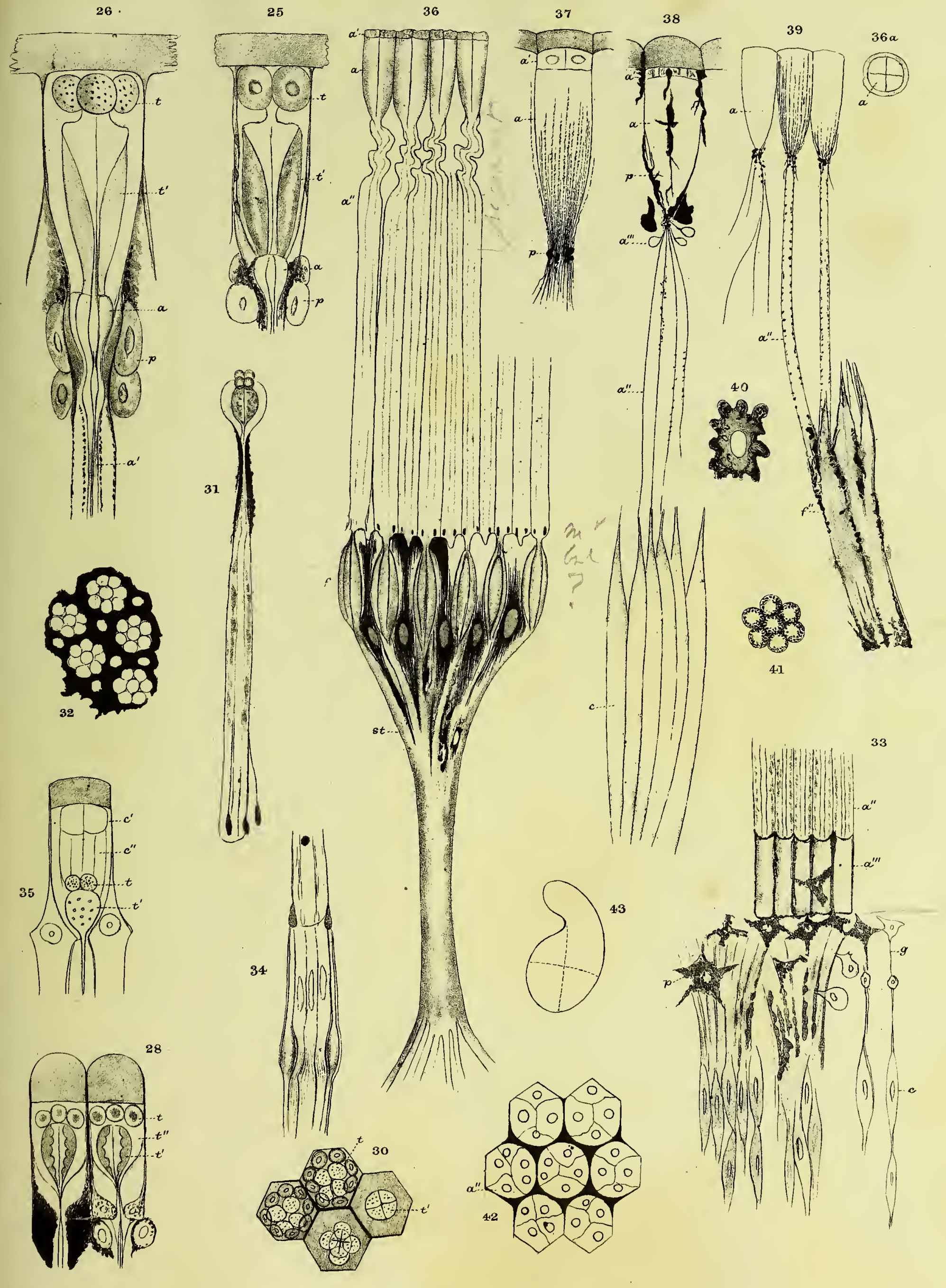

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use of exhibitors. Besides the engine which supplied power in the machinery gallery last year, an engine is being erected in the new gallery which is being put up along the north side of the old South Gallery, as described in the *Journal* of the Society of Arts for January 30. A third engine will also be provided, which will drive machinery in one of the Foreign Courts. It will thus be seen that those visitors who have mechanical tastes will be amply provided for.

As regards the prospects of applied chemistry, we are not able to speak so confidently. Probably the completeness of this portion of the show will almost entirely depend on the success of the efforts which are being made by the Society of Chemical Industry to secure a collective exhibit. The announcement made by the executive at the outset, that it was desired to show processes rather than products, is believed to have kept back many manufacturers from seeking to show specimens, while it is obvious that but few chemical processes could conveniently be carried on in an exhibition gallery. Possibly this rule might have been abrogated as regards the chemical section, and we believe that no attempt will be made to enforce it with reference to the collection of the Society of Chemical Industry, in which it is proposed that the information required shall be given by means of a collection of pictorial diagrams, exemplifying some of the more interesting or more important chemical operations.

As our readers are aware, a similar work is being undertaken by the Physical Society in the class devoted to "Philosophical Instruments and Apparatus," though in this case there will be less left for the society to do, since the principal makers of apparatus have come forward in sufficient numbers to ensure a good representative collection. The object, however, of the Society in exhibiting has been not so much to supply deficiencies, as to show the work which has been done by its own members. We believe that the Kew Observatory and the Meteorological Society will also be among the exhibitors, the latter in their old place in the grounds. Besides this, a very interesting exhibit is promised—namely, a fully fitted observatory, which we understand one of our best known makers had offered to fit up.

In the class devoted to Photography, which comes next both in the classification and in actual position in the galleries to the philosophical instruments, the Photographic Society has undertaken to form a collection of apparatus and specimens not likely to be shown by makers. It appears that the Society intend to go a little beyond the precise limits of the Exhibition, and to show a collection of examples illustrating the entire progress of photography from the inventions of Niepce and Daguerre, and it may doubtless be assumed that in so special a case no objection will be raised, especially as but a very small space indeed, and that only on the walls, will be required for what cannot fail to prove a most instructive and interesting collection.

The progress which has been made in electric lighting has indeed been sufficiently illustrated in the exhibitions of last and of the preceding year; in fact, the Health Exhibition offered almost the only public example of any progress at all in England. Doubtless the lesson will be repeated this year, and on a more extended scale, for we learn that considerable additions are being made to the arrangements for electric lighting of the buildings, while it is intended to use the light also for the garden illuminations, an improvement due to the energy of Sir Francis Bolton. If this idea is carried out on the plan which we understand is intended, the instantaneous lighting up of the myriad incandescent lamps by which the gardens are to be illuminated will certainly be one of the most popular, and one of the most wonderful, sights in London next summer.

The above remarks refer only to the English portion of the Exhibition. How much will be contributed by foreign countries it is not yet possible to ascertain. Thanks doubtless to the efforts which were made by certain of the members of the British Association who were in the States last year, the American Court promises to be well filled, and it must be admitted that in the present Exhibition, if we get American ingenuity well represented, we shall not very greatly miss the contributions of other countries, though we hope, all the same, that these will not be lacking.

THE RETINA OF INSECTS

IT might have been thought impossible for any one who has studied the eyes of Arthropods to doubt that the so-called retinulæ are really the nerve-end cells of the eye, and correspond with the rods and cones of the vertebrate eye. The evidence in favour of this view accumulated by the researches of almost every observer, including such eminent authorities as Johannes Müller, Leydig, and Grenacher is so overwhelming that of late years no one has thought fit to dispute it.

Mr. Lowne has, however, at last attempted to overthrow this theory, and in a paper just published in the *Transactions* of the Linnean Society, vol. ii. part ii., on "The Compound Vision and the Morphology of the Eye in Insects," has brought forward certain statements to prove that all the parts of the eye in front of the basilar membrane are dioptric, whilst the true (?) retina is situated behind it.

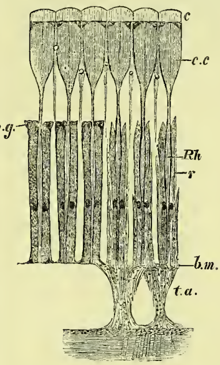


Fig 1.

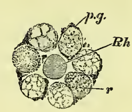


Fig 2.

Fig. 1.—Section through the eye of Squilla, showing the distribution of the ultimate nerve fibrils to the retinulæ. The Ommatidia to the left of the figure are drawn with their accompanying pigment cells (*p.g*) complete; in the three to the right these are omitted in order to show more clearly the distribution of the nerve fibrils; *c*, corneal facets; *c.c*, crystalline cone: *rh*, rhabdom; *r*, retinula; *b m*, basilar membrane; *t.a*, terminal anastomosis of optic nerve fibrils supplying the retinulæ.

Fig. 2.—Transverse section through the ommatidium of Squilla, showing the seven retinula cells surrounding the central rhabdom. The retinulæ are seen to possess a considerable amount of granular pigment, which is unevenly distributed in the different cells.

To one who has been devoting considerable time and attention to the eye of Arthropoda, this proposition is particularly striking and unexpected, and many points at once occur which show that it is untenable.

In the first place it is untenable because we have ample evidence to show that the original theory is the true one. The nerve-end cells throughout the animal kingdom have certain definite characteristics. They are the cells in which the ultimate fibrils of the optic nerve terminate, and no nerve fibrils have ever been seen to leave them to supply other parts of the eye; and, in the second place,

they are always pigmented either by a diffuse fluid "retinal purple," or by pigment in granules, or both.

In both these particulars the retinulæ of Arthropoda resemble the nerve-end cells of other animals.

It is hardly necessary to point out that Leydig, Max Schultz, Grenacher, and many others, have traced the optic nerve fibrils to the retinulæ. I have in my possession several series of preparations showing this both in insects and Crustacea, and any one can readily see this for himself by making even clumsy sections through the eye of Squilla.

In Fig. 1 I have figured the nerve fibrils of the eye of Squilla perforating the basement membrane and entering the retinulæ, and in Fig. 2 a transverse section through the rhabdom and retinulæ showing their relat ve position and numbers.

A special feature of the retinula is that it is always pigmented. In specimens hardened in spirit a granular pigment may be seen in the retinula cells, which is usually of a light-brownish colour and very unevenly distributed (Fig. 2). But in addition to this granular pigment, the retinulæ contain a true retina purple, which fades upon exposure to the light. This was discovered in 1864 by Leydig[1] in the following genera of Insecta:—Procrustes, Scarabæus, and Pieris, and in Astacus among the Crustacea. I have also seen it in *Musca vomitoria*, and have now no doubt that it exists in the Arthropod eye generally.

So far, then, I think it must be admitted that both anatomical and physiological considerations tend to prove that the retinula is the nerve-end cell of the Arthropod eye.

When we turn to morphology, too, we have confirmatory evidence that this is the case.

In the ocellus of the water-beetle larva the retina is a simple cup of pigmented hypodermis cells, in which the optic nerve fibrils may be readily seen to terminate. These cells are most certainly homologous with the retinula cells of the so-called "compound" Arthropod eye, as has been already shown by Grenacher in his important treatise, "Untersuchungen über das Sehorgan der Arthropoden" and elsewhere, and confirmed by the more recent researches of Lankester and Bourne upon the eyes of Limulus and the scorpions.

The researches of Claparède and Weismann on the development of the eye of Arthropods confirms the deductions of morphology, by proving that the cells which ultimately form the retinulæ are specially modified hypodermis cells, and at an early stage come into connection with optic nerve fibrils. If any further evidence were required to confirm this homology it can be readily obtained by studying the eyes of very young cockroaches, in which the retinulæ at the periphery of the eye are formed from specially modified and deeply pigmented hypodermis cells.

But it is tedious and unnecessary bringing evidence of this kind to confirm a theory which is already fully established in the minds of most naturalists. In fact we have here an instance in which morphology, physiology, comparative anatomy, and development combine to establish an homology, and consequently we must definitely assert that the retinulæ are the nerve-end cells throughout the Arthropoda. But what is the meaning of Lowne's bacillar layer behind the basilar membrane? and does it exist in all Arthropods?

It is perfectly true that behind the basilar in many Diptera, Coleoptera, Lepidoptera, and Hymenoptera there is a layer composed of a number of small cylindrical masses which has a superficial resemblance to the rods of the Vertebrate eye, but Mr. Lowne did not *discover* this layer in any sense of the word, for it was perfectly well known to Leydig, who figured it in *Formica rufa*, *Dytiscus marginalis*, and *Sphinx ligustri* (*vide* Leydig's Tafeln, viii. ix. x.). The little cylindrical masses cannot be regarded as cells, nor rods, nor bacilli, for each one of them is composed of a very fine reticulum of nerve fibrillæ which is in direct communication with the optic nerve fibrils behind, and the terminal anastomosis of the optic nerve fibres in front. In fact, these "bacilli" of Lowne are connected with nerve fibrils on both sides, and thus differ from "nerve-end cells" in one of their two fundamental characters.

[1] Leydig, "Das Auge der Gliederthiere." Tübingen, 1864.

Very often, too, this layer is quite devoid of any pigment (Apis, Eristalis, Bombyx, Squilla, &c.), and no one has ever yet been able to demonstrate the presence of retina purple in this region.

Another important difficulty in the way of accepting this theory, too, is the fact that this layer is not always present (Periplaneta, Nepa), and in all Crustacea and many insects it cannot be divided into separate bacilli.

I have lately paid considerable attention to this part of the optic tract, but must defer a fuller explanation of the meaning of it until I am able to publish my paper in the *Quarterly Journal of Microscopical Science*, when I shall be able to illustrate my researches by several figures. To summarise, however, the evidence against this layer being composed of nerve-end cells: We find that it is certainly not homologous with the retina of other animals; optic nerve fibrils both enter and leave it; it is devoid of retina purple or of any other form of pigment in many Arthropods, and finally it is absent as a bacillar layer in many insects and in all Crustacea. In fact we can bring as much evidence to prove that this is not the retina as we can to prove that the retinulæ are the true nerve-end cells.

At the conclusion of his paper Mr. Lowne says, in referring to a recent memoir of Justus Carrière of Strassburg, "He remains, however, a disciple of established views, and has not given the retinal layer nearly so much attention as it deserves." I have given the retinal layer as "much attention as it deserves," and must also claim to remain a "disciple of *established* views."

SYDNEY J. HICKSON

RORAIMA

A TELEGRAM has been received at Kew giving the welcome news that Mr. Everard F. im Thurn has at last ascended Roraima. This has been the cherished object of botanical exploration in South America for the last quarter of a century. The expenses of Mr. im Thurn's expedition have been borne in equal shares by the Government grant of the Royal Society and the Royal Geographical Society.

The latest news from Mr. im Thurn was in a letter dated December 6 from the south side of the mountain, and the following passage describes the position immediately before the final attack:—

"Before we came to Roraima itself we had four days walking through a purely savannah, but most glorious country, and over splendid mountain passes, guided by an Arecoona who said, villain that he is, that he knew the way to Roraima. But at a village marked on the map as Ipelemonta, on the Aroopa River, and with a considerable mountain pass still between us and Roraima, our villain guide at last admitted that the road for some distance had been quite new to him, and that he now knew not how to proceed further. However, at last we procured a guide, and came, in some four hours, out of our difficulties at Ipelemonta (its real name, by the way, is Toorarking), into this inconceivably magnificent valley, and are installed in a village on the actual southern slopes of Roraima itself.

Yesterday Perkins and I ascended the slope of Roraima to a height of 5600 feet to a most beautiful spot—a very garden of orchids and most beautiful and strange plants. To-morrow, after despatching the bearer of this scrawl, we

How Thought Presents Itself among the Phenomena of Nature

In your paper of the 5th you give a short abstract of a recent lecture at the Royal Institution by Mr. G. Johnstone Stoney, on the question "How Thought presents itself among the Phenomena of Nature." In this abstract I observe an assertion which is quite new to me, and, I must add, quite unintelligible. It occurs in the first paragraph. The assertion seems to be that there is an absolute distinction between molar and molecular motion, inasmuch as that, in the case of molecular motion there is no authority for the conviction that there must be some "thing" to be moved. The conception of motion involves the conception of matter as a necessary or inseparable concomitant—although the abstract idea of motion may, in a sense, be separately entertained. Is there any difference in this respect between molar and molecular motion? A molecule is a group of atoms, and an atom is only conceivable as an ultimate particle of matter. I hope that some further explanation may be given upon this point, which is one of the highest interest and importance, both as a matter of physical and of metaphysical speculation.

Inverary, March 8 ARGYLL

The Compound Vision and Morphology of the Eye in Insects

Mr. Sydney Hickson, in your issue of February 12 (p. 341), makes certain statements concerning my paper in the *Transactions* of the Linnean Society on this subject. I will not follow Mr. Hickson through his entire article, as I conceive it is sufficiently refuted by my paper itself. He says: "It would be tedious to bring evidence of this kind to confirm a theory which is already fully established." I would ask Mr. Hickson if anyone can explain the vision of the compound eye intelligibly on the received theory? I would also remind your readers that Prof. Huxley, writing of the crayfish in 1880, accepted the view with extreme caution; he said, "The exact mode of connection of the nerve fibres with the visual rods is not certainly made out;" that Claparède never accepted it, and Max Schultze admitted that there were grave physical difficulties in the way of its acceptance.

Mr. Hickson is very anxious, apparently, to deny me what I never claimed—*i.e.* the discovery of a layer of definite structure beneath the basilar membrane. What I do claim is the discovery of the nature of its elements. I deny, in my paper, that the optic nerve passes through these structures, and I deny that these consist of a fine reticulum of nerve-fibres. These are questions of fact and observation, not of theory or deduction. If I am wrong, I am wrong. But the way to test my work is by working out the eye as I have worked it out. I have spent nearly ten years in this work, and I do not expect to have my views generally accepted for another ten years.

The absence of pigment and retinal purple is a secondary question. I do not know, nor does any one know, whether there be retinal purple or not in this layer. I admit that pigment is absent in the retina (my retina) of some insects and crustaceans, and I have recorded the fact. I am not yet convinced that we can say vision is impossible without it. Albinos have vision undoubtedly in the absence of retinal pigment. He would be a bold man who asserted that vision could not be effected without pigment in the retinal region. The colourless collodion film of the photographer is affected; why not retinal rods? Here, again, it is a question of fact, not theory.

The presence of pigment proves nothing with regard to the function of the great rods, any more than it shows that the iris of a vertebrate is sensitive to light.

The absence of my retinal layer in Periplaneta and Nepa is imaginary on the part of my critic, for I have examined it carefully in both, and I figure the elements from the former. I maintain that the same structures exist in all the crustacea, although they are short and more difficult to demonstrate.

Again, in the morphological question my views are not fairly stated by Mr. Hickson. I admit his facts, but deny his deductions. The hypodermis forms the dioptric structures, as the epidermis of the vertebrate forms the lens; my contention is that the retina in the insect, like the same structure in the Vertebrata, is developed as an outgrowth from the nervous system.

BENJAMIN THOMPSON LOWNE

65, Cambridge Gardens, Notting Hill, W., February 23

I do not wish to undertake a lengthy controversy with Mr. Lowne on the question of the retina of insects, but I cannot refrain from making a few remarks on the letter you publish above.

I am afraid Mr. Lowne has misunderstood my criticism when he asks me "If any one can explain the vision of the compound eye intelligibly on the received theory?" My criticism was not meant for any theory of pure optics, but for the theory that the retinulæ are not the true nerve-end cells.

Mr. Lowne's statement that albinos are devoid of retinal pigment is not strictly accurate, for Kühne pointed out, and any one can see for himself, that all albino rabbits and other vertebrates possess a true retina purple. Moreover, the rods of Cephalopods and of Pecten, which seem to be devoid of pigment in spirit specimens, possess, as Hensen has pointed out, a true retina purple. In fact, I know of no exception to the rule I laid down—namely, that optic nerve-end cells are pigmented, and I should be glad if any of your readers could point out any exceptions to it.

Mr. Lowne's reiterated statement that the optic nerve fibrils do not end in the retinulæ is, as I said, contrary to my own observations. I have submitted my preparations to several eminent naturalists, who agree with me in my account of their distribution. I shall be happy to submit them to any others who may feel interested in this matter.

The other statements in my notice which Mr. Lowne controverts I will not refer to again here, as they will be fully explained and illustrated in my forthcoming paper in the *Quarterly Journal of Microscopical Science*, the proof-sheets of which I have now in hand. SYDNEY J. HICKSON

Anatomical Department, Museum, Oxford, February 25

Civilisation and Eyesight

In connection with Lord Rayleigh's letter in NATURE, p. 340, on the above subject, I venture to hope that the following may be of interest:—

In the "Expression of the Emotions" the late Mr. Darwin quotes some observations—if I recollect correctly—by Gratiolet tending to show that, under the influence of *fear*, the pupils of animals' eyes dilate. Observations extending over some years have convinced me that fear is undoubtedly capable of thus causing dilation of the pupils (see Dr. Hack Tuke, "Influence of the Mind on the Body"); and in general literature, such as travels, novels, &c., I have met with many instances in which the eyes of both men and animals under this condition have been so described by the writers.

Is dilation of the pupil under the influence of fear to be explained on the assumption that the increased aperture of the eye enables a more effective scrutiny of the object causing terror, and has thus been of service in the struggle for existence?

An answer to this question is not easy to give, for, although dilation of the pupil under the influence of fear may have originally been of direct service to an animal, yet this condition may in time have come to be associated with other emotions in which it is not so easy to trace any such direct benefit.

Observations upon the subject are by no means easy (varying light, for instance, varies the aperture of the eye), but in the course of my observations I became much inclined to believe that other strong mental emotions besides fear (*e.g.*, joy or pleasure) may be capable of giving rise to dilated pupils.

Charlotte Brontë, in "Jane Eyre," is one of the only writers who associates a dilated pupil with other emotions than fear. Here is the sentence:—"Pain, shame, ire, impatience, disgust, detestation, seemed momentarily to hold a quivering conflict in the *large pupil dilating* under his ebon brow."

It is to be feared that the experimental investigation of eyesight with artificially contracted or dilated pupils is scarcely practicable, for drugs, such as atropine or eserine, act not only on the pupil, but also on the power of accommodation for distance. J. W. CLARK

Liverpool, February 21

P.S.—I see Dr. M. Foster, in his "Text-Book of Physiology," mentions the dilation or contraction of the pupil which attends the adjustment of the eye for distant or near objects respectively, and also its dilation "as an effect of emotions." It thus seems highly probable that strong and very different mental emotions may give rise to dilated pupil. Dr. Herdman has suggested to me, as an explanation of this, that an intens

excitation of one brain centre may possibly act in the same way as a direct inhibitory impulse by partially paralysing an adjacent centre.

The Forms of Leaves

THERE are several points in Sir John Lubbock's lecture (NATURE, February 26, p. 398) which seem to invite some little criticism. That "the size of the leaf . . . is regulated mainly with reference to the thickness of the stem" seems somewhat self-evident, as a large leaf must have a large stem to carry it, as, *e.g.*, may be seen by comparing the slender shoot of a Deodar with a cabbage-stalk; but he adds: "The size once determined exercises much influence on the form." This is a *deduction* which seems to require *verification.* Sir John gives the area of a beech-leaf as about 3 square inches, but the form remains the same whatever the size. Size rather depends on vigorous growth, as in the following instances: *Populus alba* leaves on a vigorous basal shoot were $6\frac{1}{2} \times 3\frac{1}{2}$ inches, the diameter of the shoot being $\frac{1}{8}$ inch; on the upper branches of the same tree many leaves were only $1\frac{1}{2}$ to $2\frac{1}{2}$ inches long, the diameter of the shoot being also $\frac{1}{8}$ inch. Similarly growing oak leaves of the same shape were 6×3 inches and $2 \times \frac{3}{4}$ inches respectively. An *Aucuba japonica* bore rounded leaves on a basal shoot $4 \times 3\frac{1}{4}$ inches, but those on the stem were 4×1 inch. In this case, as in other plants with (normally) dimorphic leaves, as ivy, it is difficult to see what connection there is between size and form. Indeed leaves of every degree of superficial area can be found amongst the lobed ones on the climbing stem of ivy, and the entire ones of the flowering branch. Sir John adds that "the form of the inner edge [of the beech] . . . decides that of the outer one." He does not seem to have verified this deduction. The two edges are symmetrical in this leaf, but they are not so in the elm and lime. How will the inner edge explain the cause of their obliquity? If, however, the *buds* of the lime be examined, a more probable cause (as it seems to me) will be discovered in the conditions of development. He describes the *Eucalyptus*, when young, as having "horizontal leaves, which in older ones are replaced by scimitar-shaped phyllodes." Bentham and Hooker say of *Eucalyptus*: "Folia in arbore juniore sæpe opposita, in adulto pleraque alterna," but makes no mention of phyllodes. Speaking of evergreen leaves, he says: "Glossy leaves have a tendency to throw [snow] off, and thus escape, hence evergreen leaves are very generally smooth and glossy." This sentence appears to imply that such leaves are glossy in anticipation of snow! a deduction which certainly requires verification. Again: "Evergreen leaves often have special protection . . . by thorns and spines. Of this the holly is a familiar illustration; and it was pointed out that in old plants above the range of browsing quadrupeds, the leaves tend to lose their spines and become unarmed." The inference the reader draws from this is that when the holly grows out of reach of browsing animals it has no necessity to produce prickly leaves, and so changes them accordingly, thereby implying that unarmed leaves were in some way preferable. This is another instance of deductive reasoning which requires verification, for it seems to be attributing to the holly a very unexpected process of ratiocination! But it is not at all usual for hollies to do this. I have several from six to nearly twenty feet high, and not one has borne an unarmed leaf. Though my cows do not touch a holly hedge, yet one young bush lately planted has taken their fancy, and they have bitten it all to pieces. On the other hand one bush (in the garden), a variety with unarmed foliage, occasionally throws out a branch with prickly leaves, though the cows are not admitted where it grows.

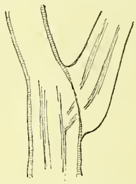
"Fleshy leaves were principally found in hot and dry countries, where this peculiarity [*sic*] had the advantage of offering a smaller surface, and therefore exposing the plant less to the loss of water by evaporation." Surely the usual explanation, that it is the thick cuticle which prevents rapid exhalation is a better reason than Sir John's deduction from the small size of the leaves? Speaking of aquatic plants, he says that the submerged "cut up" leaves of such plants presents a greater extent of surface;" and adds that "such leaves would be unable to support even their own weight, much less to resist any force, such as that of the wind.." I should be glad to know if he has verified the first statement by actual measurements; for an *à priori* assumption leads one to fancy that a complete leaf would have a greater surface than one represented by its ribs and veins only. With regard to the second and third statements a "natural experiment" completely refutes his deduction, for I know a place where a small pond dried up last summer, and a large portion of the ground was covered with a dense velvet-like carpet, composed of the *erect* filiform branchlets of the "cut-up" leaves of *Ranunculus aquatilis*, which had become modified by their new medium, and perfectly adapted to enjoy an aërial existence.

In offering these few criticisms for Sir John Lubbock's consideration, I would venture to remark that he seems to have followed too closely in the deductive methods of another writer on leaves, and which called forth the following remark from Prof. Lankester:—[He] "gives us hypotheses, suppositions with insufficient evidence, and deductions from the generalisation of Evolution, but he is relatively deficient in 'verification'" (NATURE, vol. xxviii. p. 171). GEORGE HENSLOW

Drayton House, Ealing

The Fall of Autumnal Foliage

MR. FRASER alludes to "the unpursued inquiry into the cause of leaves falling in autumn" (NATURE, February 26, p. 388), and I do not find it mentioned in Sach's "Text Book"; but Dr. Masters, in Henfrey's "Elementary Course of Botany," fourth edition, p. 515, speaks of "a layer of thin-walled cells being formed across the petiole," but does not say whence this layer is derived. Duchartre, however, gives a pretty full account of opinions up to 1877 ("El. de Bot.," deux. éd. p. 443), which he reduces to two, viz. Schacht's, who attributes it to a growth of periderm, and that of Mohls, who recognises a special layer which he calls *couche séparatrice*, considering the peridermic layer as being often, but not always formed. Subsequently, M. Ledgeganck



examined different plants and corroborated Schacht in regarding the periderm as the *cause prédisposante*, and cold to be the *cause efficiente*, which contracts "le tissu de la base du pétiole, spongieux, aéré, élastique à un degré beaucoup plus considérable que celui du coussinet." From my own observations on the horse-chestnut, ash, &c., it appears to be in these clearly a continuation of periderm produced by the phellogen of the branch, which invades the base of the petiole, till it meets in the middle, cutting right through the fibro-vascular bundles of the petiole. As this suberous layer dies, the leaf necessarily falls off. But as long as a leaf is in vigorous health it would seem to resist this invasion, and last longer, as do evergreens. I inclose a figure I possess of a slide showing the process in the horse-chestnut.

Drayton House, Ealing GEORGE HENSLOW

Forest-Trees in Orkney

IN NATURE of February 26 (p. 388) Mr. A. T. Fraser says that "a peculiarity of Caithness and the Orkney and Shetland Islands is that no forest-trees can be got to grow," and he proceeds to explain this by the preponderance of polarised light. As far, at least, as Orkney is concerned, I am prepared to rebut this calumny. It is true that forest-trees are not the striking feature of the Islands, but they do occur. At Binscarth, between Kirkwall and Stromness, there are willow, ash, sycamore, and Scotch fir. They require to be protected—from the wind, I presume, and not from the light—by hedges of bour-tree (elder). In the street at Kirkwall itself there is a fair-sized sycamore.

Trinity College, Cambridge JAMES CURRIE

YOUR Indian correspondent, Mr. A. T. Frazer, can hardly be acquainted with the primitive jungles of Southern India, or he would have observed that there, at one and the same time, the aspect of all the four seasons is displayed in the vegetation.

retinal receiving area. It is, however, a noteworthy circumstance that these natives are able to pass from the bright tropical glare outside their dwellings to the dark interiors, and *vice versâ*, without showing the temporary derangement of vision which the white man experiences whilst the iris is adapting itself to the new condition. H. B. GUPPY

17, Wood Lane, Falmouth, March 30

Mr. Lowne on the Morphology of Insects' Eyes

IN reference to the discussion between Dr. Sydney Hickson and Mr. Benjamin Lowne, I beg to state that I have been favoured by both of those gentlemen with opportunities of carefully studying their preparations, and I feel it to be my duty to state that in my judgment Mr. Lowne's preparations do not justify the conclusions which he has based on them, and are, in fact, not made with that skill and knowledge of modern histological method which is necessary in order that trustworthy conclusions may be obtained. On the other hand, Dr. Hickson's preparations are thoroughly satisfactory as examples of histological manipulation. Dr. Hickson supports the accepted view as to the termination of the optic nerve-fibres in the nerve-end cells of the retinulæ. Mr. Lowne denies this connection. I have no doubt that such a connection cannot be readily observed in Mr. Lowne's preparations. At the same time I have no doubt whatever that this is because the preparations are badly made. Mr. Lowne's preparations fail to show many other simple features in the structure of the insect's eye, which are readily seen in preparations made by the application of methods now recognised and approved, but not made use of by Mr. Lowne.

I am sorry to see the resources of the Linnean Society employed in publishing a memoir the conclusions of which, although startling in their novelty, are undeniably based upon the mistaken interpretation of defective preparations.

I think it is important that the Fellows of the Linnean Society should know whether the memoir now published is the same which was read a year or two ago at the Royal Society, and whether the Council of the Royal Society took any steps to ascertain the value of Mr. Lowne's preparations, or came to any decision as to the fitness of Mr. Lowne's paper for publication.

March 14 E. RAY LANKESTER

On the Terminology of the Mathematical Theory of Elasticity

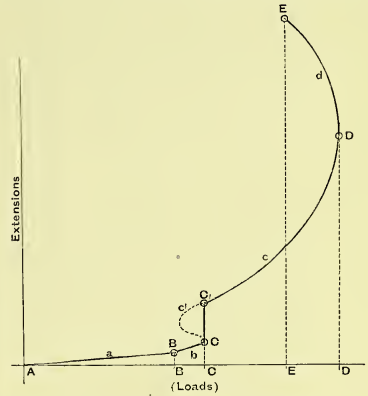
ENGINEERS quite as much as "elasticians" have reason to want some such terminology as that sought by Prof. Pearson (NATURE, vol. xxxi. p. 456), and have equal reason to be indebted to him for undertaking the work which he has at present in hand, which seems already to have given results of practical value as great as their scientific interest.

As I have for some years made a study of the physical side of the problems mentioned by him, I should be glad to make some suggestions as to terminology as contributions to the discussion of the subject in your columns. I will confine what I have to say to what may be called ductile materials (such as wrought iron, ordinary steel, copper, &c), because in these only the whole phenomena are visible. The behaviour of such material in tension is illustrated by the accompanying figure, in which stresses are measured along the horizontal, and strains along the vertical axis.

It is extremely rare to obtain a piece of raw material already in a *state of ease*. *Wire*, of course, is highly strained by its process of manufacture, but that even ordinary bar and plate is also slightly strained, is shown in the manner mentioned by Prof. Pearson. Such initial strains as become visible as *set* by the first stretching up to any load (within limit of elasticity) disappear after one or two applications of that load. The material is then in a state of ease up to that load, but higher loads (still within the limit), on their first application, generally produce more set—the state of ease thus extending only to the stress employed to produce it. The *sets* are, along with the elastic strain, proportional to the stress, their effect being simply to lower the modulus of elasticity. Probably the process of *annealing* will bring the material into a state of ease for all loads at which such a state is possible. I propose to examine this matter further by aid, if possible, of the apparatus described by Prof. D. E. Hughes in the Inst. M. Eng. *Proc.*, 1883, p. 73. In the figure, *a* represents this *condition of perfect elasticity* (maximum state of ease being presupposed) and B, the superior limit of this condition, is the mathematical *limit of perfect elasticity*.

After B comes a stage *b*, within which the set is *not* proportional to the stress, although it still remains small; the total extension, therefore, increases faster than the stress. Occasionally this stage does not occur at all, and both its higher and lower limits seem—more than any other points in the life of the material—to be susceptible of change depending on manipulation. Accidental shock will shorten the stage considerably; very gradual loading extends it somewhat. For these and other reasons I therefore suggest that this stage be called the *condition of instability*, or of *unstable equilibrium*.

This condition terminates at C, in what I have called a "breaking-down" in the paper referred to by Prof. Pearson, in which paper I believe the phenomenon was described for the first time. This point is the one called by engineers the limit of elasticity, because it is the only one markedly visible without special apparatus. (The extension at B, on a length of 10 inches, may be about 0·01 inch; at C 0·03 inch and at C_1, same stress, it increases to 0·20, 0·25, and even occasionally 0·4 inch.) If "breaking-down point" be too crude a name, I would suggest *limit of stability*. It should be noted that the stress at this



point does not remain constant, but in reality appears to diminish as the extension goes on, as shown at c' (this dotted curve not drawn to scale), a matter on which I am at present experimenting. I should add that, during the application of load at this point, extension appears to be occurring at different parts of the length *successively*, and not at all parts simultaneously, as during conditions *a* and *c*.

In the next stage, C to D, the whole strains consist of a very small elastic portion (apparently closely following the modulus), and a very large set, increasing much faster than the stress. The test bar remains at each load practically constant in its cross-section at all points of its length, and rises in temperature instead of (as in condition *a*) cooling. I would suggest for this stage the name *condition of uniform flow*, the physical applicability of which will be obvious to any one who has seen ductile metal in this condition.

At some point, D, a maximum load is reached, and at *about* the same point (generally, I think, a little earlier, but the difference is small, and not very easy to get at with certainty) the metal begins to flow *locally*, a part becoming much more reduced in cross-section than the rest, and eventually fracture occurs at this place under a less load than D, but with a greater extension, as at E. This final stage, *d*, might be called *condition of local flow*. The loads D and E (as Prof. Pearson suggests) would be *maximum* and *terminal* loads respectively). (Their difference was first pointed out, I think, by Mr. Daniel Adamson's experiments, *Journal* I. and S. Inst., 1878). The maximum *intensity* of stress

ethnography. The authoctonous population of the Philippines, the Negritos, were driven back by two Malay invasions, and are now to be found only in isolated remnants scattered throughout the islands of the archipelago. By the first invasion the Negritos were forced from the coast into the interior, where they remained undisturbed until the second Malay irruption. This drove the first Malay invaders in their turn from the coast, and the descendants of the new comers still occupy the ports and harbours to this day. The Negritos were either destroyed by wars with the first Malays, or completely absorbed by marriage with them, that now no tribes of them are to be found. The Malays of the first invasion came from Borneo, and are found to-day in the mountain districts of Luzon, under various tribal names, such as the Tingianes, Igorrotos, Guinanes, Apayos, Abacas, Calnigas, Gaddanes, &c.; while the second invaders, now known as Tagals, Pampangos, Visayas, Ilocanes, Cagayanes, &c., inhabit the coast regions, where they were found by the Spaniards in the third quarter of the sixteenth century. Naturally the various tribes were unable to prevent being influenced by each other, as well as from without, and to this we must attribute similarities in many respects, and especially in religion, which mark the Malays of the whole archipelago. Allowance too has to be made for the influence of the Chinese, perhaps also of the Japanese, on the tribes living on the coast long prior to the Spanish invasion. The inhabitants of the coast, the Malays of the second invasion, for the most part profess Christianity now, and are well known, but the pagans of the interior, the Borneo Malays, who, according to Prof. Blumentritt's theory, formed the first invasion, have never been thoroughly investigated, and this circumstance led Dr. Meyer to spend three months among the Igorrotos. The appendix in which he records his observations is very full. It discusses the name and extent of the Igorrotos, their territory, and its climate, their build, mode of dressing the hair, and tattooing (which is far more elaborate than that of even the Japanese grooms, and is probably the most complicated in the world), their dress, ornaments, weapons, villages, huts, agriculture, and cattle-breeding, food, and drink, domestic utensils, art, tools; customs at birth, and marriage, and death; their priests and religion; head-hunting, war customs, festivals, language, modes of reckoning time and numbers, and their myths and sagas. Finally comes Dr. Virchow's account of an Igorroto skull, and a brief vocabulary. It is this portion of the work which renders it one of scientific interest, and prevents it from being a mere amusing account of the modern grand tour. The numerous illustrations which it contains of the tattooing ornaments, utensils, and the like, add greatly to its value. The Igorrotos are among the disappearing peoples of the earth. They leave the impression of having once possessed a higher culture; their manufactures now are far below those of even half a century ago, and Dr. Meyer thinks that, like every primitive race brought into direct contact with European civilisation, nothing can save them from ultimate extinction.

LETTERS TO THE EDITOR

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Molecular Dynamics

I THINK there must be some mistake in Prof. Forbes' report of Sir Wm. Thomson's remarks as quoted in NATURE of last week (p. 461) upon the rate of wave-propagation on Maxwell's electro-magnetic theory of light. From the end of the last quotation one would suppose that Sir Wm. Thomson intended to convey that the rate of wave-propagation that Maxwell's theory asserted to be the same as that of light, was the rate of propagation of a variation of a current in a conducting wire. Now Sir Wm. Thomson cannot, I am sure, have intended to convey any such mistaken notion. Maxwell carefully guards against any such mistake by pointing out that conduction of electricity is of the nature of diffusion, and not of a wave-propagation, and so has no definite velocity. What Maxwell has calculated is the rate of propagation of disturbances in *non-conductors*, and not in conductors. It is the rate at which the disturbances, produced in the way considered by Sir Wm. Thomson in the preceding part of this quotation, would be propagated by transverse vibrations. Of course, as Sir Wm Thomson asserts, something analogous to a longitudinal vibration may co-exist with these, but Maxwell's theory shows that a medium which would transmit only transverse vibrations would explain electric and magnetic phenomena.

GEO. FRAS. FITZGERALD

40, Trinity College, Dublin, March 23

* [The passage quoted by Mr. Forbes is correctly reported. A more full explanation of this subject will be found in Nichol's "Cyclopædia," second edition, 1860, article, "Electricity, velocity of;" reprinted in vol. ii., art. lxxxi., of my collected mathematical and physical papers.—W. T.]

Civilisation and Eyesight

HAVING read with much interest the recent correspondence in NATURE on this subject, I am forwarding the results of some observations which I recently made to determine the degree of acuteness of vision possessed by the natives of the islands of Bougainville Straits, in the Solomon Group.

I examined the powers of vision of twenty-two individuals who were in all cases either young adults or of an age not much beyond thirty. For this purpose I employed the square test-dots which are used in examining the sight of recruits for the British army, and I obtained the following results:—Two natives could distinguish the dots clearly at 70 feet, one at 67 feet, two at 65 feet, three at 62 feet, four at 60 feet, two at 55 feet, three at 52 feet, four at 50 feet, and one at 35 feet. The conclusion at which I arrived was that 60 feet represented the average distance at which a native could count the dots—a distance rather greater than that at which they should be placed to test the normal powers of vision, viz. 57 feet.

Of these twenty-two natives I came upon only one whose vision seemed at all defective. In this instance—that of a man about thirty years old—the nature of the cause was sufficiently indicated by the prominence of the eyes and the nipping of the lids, especially when the sight was strained by trying to count the test-dots at a distance. The limit of distance at which this man could count the test-dots was 35 feet. The question which presented itself to my mind in this case was, whether a white man who could count the dots at the same distance—viz. 35 feet—would exhibit to the same degree the external signs of myopia. I might put this query into other words, and ask whether, considering the far-seeing powers of these natives, the peculiar external signs of myopia would not appear with a less degree of this defect than with the white man.

Natives of these islands are very quick at perceiving distant objects, such as ships at sea. I was often much impressed by their facility in picking out pigeons and opossums, which were almost concealed in the dense foliage of the trees some 60 or 70 feet overhead. My attention was not attracted by the unusual size of the pupils; the eyes, however, have a soft, fawn-like appearance with but little expression. In conclusion, I may refer to the circumstance that the interiors of their houses are always kept dark, the door being usually the only aperture admitting light. The object is, I belive, to exclude flies and other insects from their dwellings. Coming in from the direct sunlight, I have often had to wait a minute or two before my eyes became accustomed to the change; but the natives do not experience this inconvenience. Some hours of the day they commonly spend in their houses, while at night they use no artificial light except the fitful glare of a wood fire. It would seem probable that the influence of the opposite conditions, presented by the bright sunlight and the darkness of their dwellings, would be found in the increased rapidity of the contraction and dilatation of the pupil with the enlargement, perhaps, of the

the pressure of a gas or the electric resistance of a wire "comes out" negative! To such men the recent introduction of the subjects of heat and electricity by the Board of Mathematical Studies, and the appearance of Thomson's *Electrical Papers*, Maxwell's splendid treatises, and other kindred books, have been happiness indeed. Open any one of these books, at any place, and concoct from it by whatever assumptions (however unphysical) are necessary, a problem which shall lead to an elliptic integral or a Bessel's function, and there you are! This cannot long go on without seriously impairing the progress of physical science in our great mathematical university. Mathematics is, in itself, a right noble and worthy study; but the embryo physicist should, from the first, be taught to regard it as (for him) an indispensable auxiliary only, not a source of natural (?) laws. The whole procedure is thoroughly characteristic of the Cambridge of to-day. It has, among its professors and elsewhere, many of the foremost of living physicists and mathematicians, as well as others destined in time to take similar rank:—but does not utilise them. Even its *one* real test of mathematical merit, real because conducted by such men, the Smith's Prize Examination, has just been abolished! So, it has a magnificent boat at the "head of the river," but *not one member* of that crew is sent to encounter Oxford at Putney! What can be expected, either in the boat-race or in the more arduous toiling over the scientific course, but thorough and most deserved defeat?

Differential Calculus for Beginners, with a Selection of Easy Examples. By Alex. Knox, B.A. (London: Macmillan and Co., 1884.)

THIS little book deserves hearty welcome from those who are engaged in leading forward students to the higher mathematics; not so much as a substitute for any other work at present in use, but as presenting a carefully-selected set of illustrations of infinitesimals, limits, and differential coefficients, which a student may profitably work through before entering upon the usual formal treatises on the calculus.

We know of no work in English comparable with the present since De Morgan's "Elementary Illustrations of the Differential and Integral Calculus."

The special symbols of the subject are not introduced into the work before us, attention being directed to the new principles involved in the method of the calculus; indeed, the chief aim of the author throughout is to give the learner a firm grasp of the idea of a differential coefficient—a fundamental notion which, in the minds of beginners, is usually shrouded in a haze. Care is taken to deal one at a time with the difficulties which present themselves in this subject. The book is divided into twenty sections, the latter two or three dealing with successive differentiation, Maclaurin's theorem, and maxima and minima.

But before new principles or processes are introduced, an endeavour is made to insure a precise comprehension of the meaning of terms already employed by the student. And the freshness of treatment, as well as the clearness with which the author brings before the mind the exact meaning of such terms as "point," "line," "superficies," in the first section of this book, will awaken the interest and arrest the attention of even an indifferent learner.

Many of the sections are independent of each other. There is much variety of illustration, the central principle being looked at from different points of view. A distinguishing feature is the great use made of arithmetical calculations, many examples of the method of finite differences occurring.

Besides the usual geometrical treatment based on Newton's "Lemmas," the ideas of time and motion are freely introduced, and illustrations taken from elementary kinematics.

The book closes with a set of examples worked out in full, and a series of one hundred easy exercises, the answers to which are appended. A. R. W.

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Rock-Pictures in New Guinea

A FEW years ago I mentioned in a paper in *Globus* (lxiii. 94) that Mr. Th. B. Leon had reported the existence of pictures on rocks he had seen in the Ogar and Arguni groups of islands (south part of McCluer inlet), and that the officer in command of H.N.M.S. *Batavia*, who had been charged to make further inquiries, had not been able to find them. At that time Mr. Leon's account had not been published in the regular issue of the *Batav. Genootschap.* Since then, however, explorations by Mr. van Braam Morris, whilst on his voyage in New Guinea in 1883, and by some of the officers of H.N.M.S. *Samarang*, have resulted in the discovery of rock-pictures similar to those spoken of by Mr. Leon. The papers giving an account of these explorations (including Mr. Leon's) have been published in a recent number of the *Tijdschrift voor Indische Land-, Taal-, en Volkenkunde* (xxix. pp. 582-591), and an abstract of their contents may be interesting.

One day Mr. Leon set out from the kampong (village) of Arguni, situated on the island of that name, for the purpose of fishing. In the beginning, on account of the surf, he kept at a great distance, but the third island of the group he was able to approach. He perceived the distinct representation of a human hand, painted in white, and surrounded with red spots, and other drawings in white, which appeared to be meant for letters, though traced in characters unknown to him. Afterwards, on penetrating between two other islands of the group, he saw several hands, all similar to the first, and accompanied by similar drawings. He was not able to land; he estimated the height of the place at which they were drawn on the rock to be from 75 to 150 feet above sea-level, the hands being about three-quarters of the way up, and the other figures about 10 feet higher still. The hands were of all sizes, representing those of children, of full-grown men, of giants, and were in great numbers. He fancied the characters bore some resemblance to the written signs in use amongst the *Orang Kling*, the *Orang Bugis*, and the *Orang Mangkasser*; they were certainly not *Javan* or *Malayan*. He was greatly puzzled as to how they could have come there, since the face of the rock was perfectly perpendicular, and without any projections or caverns, so far as he could perceive. The only explanation he can suggest is that they must have been done at a time when that part of the rock-surface was nearer to the level of the sea, or the outward form of the rock must have been changed on that side by losing ledges or projections by which the native draughtsmen may have approached the place. It will be readily understood that the natives attribute these drawings to *Kasuak*, the prince of evil spirits, who, in their opinion, has his dwelling in one of the small islands, and of whom they are naturally greatly afraid. On another island Mr. Leon discovered a huge stone, which would probably require half a dozen men to lift it, rudely shaped like a bullock, and surrounded with several other stones, evidently arranged on some fixed plan.

Mr. van Braam Morris says:—On September 16, 1883, I came to McCluer inlet, and was told by the native chiefs that the figures I was in search of were to be found on Arguni, or the islands to the west of it. I discovered them on a small island a few hundred yards from the mainland. The shores of both the island and the mainland rose perpendicularly from the water, and in the rocky face of the former, about 5 feet above high-water mark, the surf had eaten out an excavation from 3 to 5 feet wide, thus leaving a narrow platform, on which several small *prahus* were deposited, some of them being 3 feet long. Various figures were drawn on the rock above, especially hands, both of full-grown people and of children. A hand had evidently been sketched in outline from

a living model placed against the wall, and coloured to a depth of 6 inches all around it. The native chiefs who accompanied the Resident said that the remains of the Hill-Papuans had formerly been deposited here, but were now interred with Mahommedan rites; there were indications, however, that some *prahus* had been recently lodged on the platform.

Though the most astonishing part of Mr. Leon's report, viz. the difficulty of drawing the figures on the rock at a considerable height above the sea, is not encountered by Mr. van Braam Morris's experience, it is not proved that the latter explored exactly the same place as Mr. Leon. But just this point (the considerable rising of the islands) is most plainly stated with regard to the Ke Islands by Messrs. Alliol, Mol, van Slooten, Meijboom, and Deijl, of H.N.M.S. *Samarang*, which at the time of their visit lay off Tual (5° 37′ 30″ S. lat. 132° 44′ E. lat.), island of Little Ke. These gentlemen were invited by Mr. Langen, the head of the English settlement there, to visit with him the north-western part of the island; after having steamed for three-quarters of an hour they dropped anchor *vis-à-vis* Kalumit, a village at the base of a hill, about 200 metres high. They went to the top to see there some idols situated in a small settlement. I pass over this part of the narrative, and take it up after they had descended from the edge of the rock, where they had found a burial-place belonging to the kampong, which is on the top. A tolerably well-made flight of ironwood steps allowed the visitors to descend easily; after about half an hour's walk they came to the "necropolis."

On the rock near it they discovered representations in red of various figures—human hands, with the fingers spread out; imitations of human heads; a fight between men armed with *klewangs* (= cutlass), and other figures which they took to be representations of the evil spirits, outlines of ships, &c. Though the heads were rudely drawn, the hands, which were fewer in number, were remarkably well done. The place where the drawings are seem to be quite inaccessible to human beings. In the rock are also caverns which are rather difficult to approach. In one of them two gongs and some pieces of bamboo were found; at the entry fragments of broken glass had been spread, probably to prevent visitors from entering. It must be mentioned that the rock, from the base to the top, was covered with sea-shells. Attention is repeatedly drawn in the report to the circumstance that it seems incomprehensible how the pictures could have been drawn on the rock, which overhangs.

The natives connect the rock-pictures with the burial-place on the top of the cliff. Near the edge of the steep descent stand two houses, which serve as mortuaries, one being close to the dwellings of the natives, which are surrounded with a stone wall. These two houses are built of ironwood; on the roofs there are two pieces of wood, the one in the shape of a prow, the other in the shape of a keel. On the latter are two figures, a dog and a bird; a stick bearing a piece of white cloth is stuck into the bird's body. The walls are 4 and 3 metres, and in the shorter, which faces the sea, there are two doors, through which the coffin is carried; inside this hut they saw two coffins with fruits and a bottle of oil which had been left for the spirits.

The natives, who called themselves Hindoos or heathens, a name which of course has no ethnographical significance, but is merely used to distinguish them from their Mahommedan neighbours, said that when a dead body was placed in the hut the spirit was conducted by the bird or the dog on the roof to the caverns where it is to abide. In token of its arrival the animal draws a figure on the rock. The natives who accompanied the explorers durst not set foot within the caves.

It was also said that the bird and the dog were merely symbols. The soul of the deceased, on leaving the body, flies as a bird through the air or runs as a dog over the earth, till it reaches the abodes of the spirits—the caverns—unseen by living men. Every soul that reaches this haven draws a figure on the face of the cliff. In explanation of the contest between human beings and evil spirits in the pictures, they said that the latter try to prevent the souls from reaching the eternal dwellings; but they cannot hinder those who have led good and honest lives, though those who have done wickedly are carried off by the evil spirits.

The officers, judging from the many articles in gold and silver which were found in the caverns, concluded that they must formerly have been used by pirates as places of refuge and for hiding their stores, and that they were then nearer to the level of the water. On this view the drawings on the rocks would answer a double purpose: they would keep the superstitious from approaching the caves, and would also act as a landmark for the pirates themselves when returning from sea, and indicate to them the places where their treasure was hidden.

Without hazarding any opinion upon such incomplete accounts, I wish to state, merely by way of summary—

(1) That Mr. Leon's evidence, combined with that of the officers of the *Samarang*, would seem to indicate that the surfaces of certain islands in McCluer inlet and of the Ke group have been considerably elevated.

(2) That the rise has probably taken place at no distant date, but how long since cannot be determined until (perhaps) after close scientific examination.

(3) That Mr. Morris's explorations, taken in conjunction with the foregoing, suggest that the elevation is not a general one, but, though observed at distant points, is limited to certain islands of different groups, or even to particular sides of them.

Stuttgart, March 18 EMIL METZGER

Mr. Lowne on the Morphology of Insects' Eyes

PROF. LANKESTER appears to me to be fighting too much under cover. First he sends his lieutenant into the field, and then he appears himself, in the guise of an independent ally. But inasmuch as he has virtually accused the officers of the Linnean Society of having published a paper unworthy of a place in the *Transactions* of the Society, I feel fully justified in bringing him out into the open.

The anxiety expressed by Prof. Lankester on behalf of the Fellows of the Linnean Society, as to whether my paper was refused by the Royal Society, is manifestly insincere: he knows as well as I do, that the paper was virtually refused by the Royal Society. As Prof. Lankester is taking undue advantage of the secrecy which attaches to the office of referee, I shall state the facts with which I am personally acquainted, and I doubt not these will place the whole matter in a very different light from that which Prof. Lankester has endeavoured to shed upon it.

It is evident Prof. Lankester wishes to make it appear that the rejection of my paper by the Royal Society confirms his strictures and those of his lieutenant, and enables him safely to attack the Linnean Society under cover of the Royal. Now, I believe that every one who was concerned in the publication of my paper knew perfectly well that Prof. Lankester was the first referee to whom it was submitted by the Royal Society. Prof. Lankester wrote to me himself, and stated that the paper had been so referred. Although I then felt sure of its rejection, I should not have had any reason to complain, if the rules of the Royal Society had been carried out, and the paper had been submitted to a second, entirely independent referee. Prof. Huxley, in his opening address to the Royal Society on his election as President, stated that every paper was considered by two entirely independent referees. Now, in my case the second referee was Prof. Schäfer: I do not think it right to refer a paper to two colleagues intimately associated in the same school; and I am sure that no consultation should take place between the referees pending their decision. Yet Prof. Schäfer heard Prof. Lankester's adverse opinions expressed in my presence before he came to any decision himself—at any rate before making any report; and he confessed to me that he had no special knowledge of the literature of the subject on which he was called upon to give an opinion.

Under the circumstances I feel justified in stating that, if the Royal Society had rejected my paper, it would have been a rejection by Prof. Lankester; and I feel sure that an independent referee would have done exactly what was subsequently done on behalf of the Linnean Society.

Prof. Schäfer recommended me to withdraw my paper; I petitioned the Council of the Royal Society to allow me to do so, and the paper was returned to me. If this be a rejection, my paper was rejected.

I then presented it to the Linnean Society, and in so doing I told the Zoological Secretary everything that had happened. The result was that, after some delay, the paper was ordered to be printed in the *Linnean Transactions*.

I could hardly have conceived it possible that any scientific man could have descended to such a device in confirmation of his own views as to pretend that the Royal Society had formed an independent judgment under such circumstances. Prof. Lankester has succeeded admirably in rendering himself impersonal as a representative of the Royal Society—a feat which

would have no doubt incited his just indignation if it had been performed by his friend "Sludge," of spiritualistic celebrity.

I cannot help remarking on the coolness of Prof. Lankester's assertion, that my views are "undeniably based upon a mistaken interpretation of defective preparations." Prof. Lankester evidently thinks his opinion final—but he is bold to say it is "undeniable."

My sections have been seen and approved of by a great number of competent histologists and zoologists, and, although some of them are not so pretty as those prepared by the paraffin method which Prof. Lankester extols, they certainly show a great deal more. The paraffin method is well known to me, and I have examined a great number of slides prepared by it. I have possessed a series of sections so made in the Cambridge laboratory by an excellent histologist, and have rejected them as worthless: they show nothing but the connective tissue framework. Nerve fibres and nerve end organs are alike destroyed.

The whole question of the effect of reagents on the tissues is a wide one. The paraffin process destroys much which remains in the cocoa-butter process, first devised by Prof. Schäfer. I esteem this process far superior to that now used in the laboratory at Cambridge, and by Prof. Lankester and his assistants. I should not fear to place my specimens side by side with Prof. Lankester's before an unbiassed histologist; and I am content to wait the decision of future observers upon my work. New views are met with little favour by those who are committed to old ones, and, whether I am right or wrong, I expect no justice from a critic who shows such determined bias as Prof. Lankester.

BENJAMIN T. LOWNE

IF Prof. Lankester imagines that he has any complaint to make against the Council of the Linnean Society for having published Mr. Lowne's paper, I must decline to consider the subject with him in your columns. He is himself a Fellow of the Society, and the anniversary meeting of the Society is due next month. If he then thinks it wise to ask any questions upon the subject, I shall be in my place and most happy to answer them.

GEORGE J. ROMANES,
Zool. Sec. L. S.

How Thought presents itself among the Phenomena of Nature

IN your issue of the 12th inst. the Duke of Argyll asks, "Is there any difference in this respect between molar and molecular motion?" namely, as regards the persuasion which most men entertain that where there is motion there must be some "thing" to move. The answer to this question appears to be the very direct one that there is the following fundamental difference between molar motions and *some* molecular motions, and that it intimately concerns that belief. *All molar motions are secondary motions, i.e.* they consist in the drifting from place to place of underlying motions (and, indeed, in the case of those motions which human beings can perceive even with the utmost aid of the microscope, they consist in the drifting from place to place of vast accumulations of such underlying motions), while, in contrast to this, *there are some molecular motions which are primary—i.e.* which have no other motions underlying them, and which do not consist in the drifting from place to place of more subtile motions.

His Grace correctly expresses the common opinion in the following words—that "an atom [1] is only conceivable as an ultimate particle of matter." Now the term "particle of matter" in this statement needs to be scrutinised. As commonly understood, it means something minute which we should be able to feel or see or perceive by some of our senses were it not for the bluntness of those senses; and this, as science shows, means that *certain specific motions* are present, viz. motions of those particular kinds which are competent, indirectly and through a long chain of intermediate steps, to finally occasion visual, tactual, or some other sensation in our minds. The statement, accordingly, as commonly understood, *really* amounts to this—that no motion can be present unless certain underlying motions are also present!

But to the uninstructed apprehension the statement has quite a different meaning, a much fuller one, and one which lies outside the domain of motion. Before they have made very careful investigation, men do not know that there is no green colour in grass or hardness in a rock. They are unaware that what is really going on in the grass is not a state of greenness, but vast myriads of motions,[1] each of which is repeated about as often every second as there are seconds in thirty millions of years, which motions in the grass occasion undulatory motions around of a like rapidity, some of which occur within our eyes, and, acting upon some compound or compounds in the black pigment which lies behind the retina, produce there an effect (probably a fugitive photographic effect consisting in some chemical change of one or more of three compounds in the pigment). This change, whatever it is, excites the optic nerve to make a stir within the brain, and *it is this last motion* (which we may safely say is utterly unlike the external phenomenon, though uniformly resulting from it through the steps enumerated above), which is what determines the perception of green in our minds. Similarly, when the vast accumulation of molecular motions which is called my finger approaches that other accumulation of motions which is called a rock, these motions act on each other, and my finger is compressed upon certain nerves, exciting them to produce those motions within my brain which, though quite unlike the motions outside, are the motions that are really accompanied by the sensation of hardness. But by uninstructed minds the colour of the grass and the hardness of the rock are confidently believed to be external phenomena, and not even phenomena of motion at all, but absolutely stationary phenomena in external Nature.

Finally, we must never forget that beliefs in the human mind, whether they be pure or mixed up with errors, can neither control nor even exercise any influence whatever upon what is really taking place in external Nature, which is the object of our investigation. What is really going on in Nature is to be ascertained, so far as it can be ascertained at all, not by projecting human beliefs into external existence, but by applying whatever modicum of dry light we can win from the slow but gradually encroaching progress of scientific discovery. And the necessity for this caution is intensified where we find, as in the present instance, that the belief has resulted from the way our brains and the brains of our ancestors have grown, under the influence of an experience of motion which has been so one-sided that it has never extended to primary motions at all, nor even to any but very coarse forms of secondary motion, omitting, along with many others, all those motions, whether primary or secondary, that occasion most of our sense-perceptions; and all this, combined with suppositions about other phenomena in which these phenomena have been quite misunderstood. Scientific scrutiny, so far as it has penetrated, finds motion throughout external Nature—motions everywhere, motions underlying every phenomenon, however different from motions some of them may seem to common apprehension; and no *scientific* investigation has as yet detected anything but motions. This is the positive side of the inquiry; and its negative side is that it would be manifestly illegitimate to draw an inference about what really exists outside us from the habits of thought which have been engendered in most human minds by a narrow and one-sided experience mixed up with palpable errors. *We, therefore, are not in a position to allege that we know of anything existing in the outer world but motions and relations between motions.*

The abstract of my Royal Institution discourse, which you were so good as to publish, only attempted to give a bare statement of the successive steps of the argument with which it deals, and I fear it is too condensed for clearness; but, as I am myself persuaded that the argument is sound, I hope that your correspondent will find that a fuller account of it which I am preparing will put all its essential parts in a sufficiently distinct light.

Dublin, March 20 G. JOHNSTONE STONEY

[1] The Duke of Argyll here employs the word "atom" in its etymological sense; and it is scarcely necessary to point out that the term when so used signifies a different thing from any of the sixty-seven complex bodies known to chemists as chemical atoms, which have intricate internal motions as betrayed to us by the spectroscope, and of which the molecules of compound bodies are known to be made up. The chemical "atom" could not under any view be spoken of as an *ultimate* particle of matter.

I understand the Duke of Argyll to propose these words as a description (not of anything the existence of which has been ascertained by experimental science, but) of that substance, matter, or thing the conception of which he and most other men believe to be the "inseparable concomitant" of the conception of motion, but for the existence of which in external nature no other evidence is forthcoming than this supposed law of human minds.

Now, even if the supposed law were a law from which we could not free ourselves, it might reasonably be maintained that it proves nothing about external existence; but in truth it is not a law, but only a widely prevalent habit of mind, as is *demonstrated* by the fact that the study of nature has extricated some minds from it.

[1] The relations which the parts of motion can have to one another or to other motions are all numerical or space and time relations. Motions may be numerous, few, simultaneous, successive, straight, curved, flat, tortuous, swift, slow, periodic, continuous, linear, or pervading a volume; but they cannot be green motions or hard motions.

Magnetic Disturbance

There was a considerable disturbance of the magnetograph recorded here on March 15, and had the photographic curves been developed on that day, we should probably have predicted the occurrence of the aurora seen during the evening. The earth-currents, which are necessary concomitants of magnetic disturbances, were probably intense enough to cause the disarrangement of the cable tests referred to by Mr. Willoughby Smith.

G. M. Whipple

Kew Observatory, Richmond, Surrey, April 7

The Samsams

From a note in last week's Nature it appears that during his recent explorations in the Malay peninsula M. Delouell claims to have discovered the "hitherto unknown" Samsam people. Allow me to state in reply that I have long been aware of the existence of these half-caste Malay and Siamese communities. They will be found duly recorded and described at p. 642 of my ethnological appendix to the "Australasia" of the Stanford Series, published in 1879. They appear to be now mostly Mohammedans, speaking what is called a mixed Siamese and Malay dialect, and otherwise forming an ethnical transition between these two races.

A. H. Keane

University College, Gower Street, April 4

Meteor

Last evening (April 3) I saw a fine meteor at 8h. 21m. G.M.T. ($\pm$ 1m.). I was walking along the street at the time and looking at Algol, and so only caught sight of it during the last few moments of its apparition. Its path as observed was from α 80° North δ 2° to α 76° South δ 4°, when it disappeared behind houses. It seemed quite twice the brightness of Jupiter, and about 3′ diameter; colour, chrome yellow; duration, three seconds. It left no visible train.

H. Sadler

Clapham, April 4

STEEL GUNS[1]

The whole of this part of the Proceedings of the Naval Institute is occupied by detailed accounts of the steps taken to prepare the way for the establishment of Steel Gun Factories for the United States. We are informed that, while the rest of the world has advanced with the progress of the age, the artillery of the United States has made no step forward. Artillerists and advocates for providing adequate means of defence have laboured under many difficulties during the last twenty years, while regret is expressed that personal interests have entered so largely into the discussion of a question of such magnitude. In the House of Representatives it was declared that the fortifications of that country were in an absolutely worthless condition for all purposes of warfare.

Early in 1882 communications were opened with the owners of the chief foundries and steel works of the United States, but no firm could be found which had ever made steel guns.

At length the President of the United States was authorised and required to select six officers of their army and navy to examine and report respecting the necessary navy-yards and arsenals. Accordingly, the President named six officers (April 2nd, 1883) to form the Board of Gun Foundry, and one of their number, Lieut. W. H. Jaques, U.S.N., was elected secretary to the board. Their report was dated February 16th, 1884. The Board found it necessary to seek information in Europe, and make visits to England, France, and Russia, in order that they might reply satisfactorily to the Act of Congress. There they were well received, and had every facility afforded them in making their inquiries. The aim of Lieut. Jaques, U.S.N., in his communication to the Naval Institute, was to show the necessity of steel gun factories to the United States, to extend the information collected, and to provide a book of easy reference to the details of modern ordnance. He has produced a work which ought to warn and instruct us.

The Board in their Report give an account of the introduction of the coil system of building up guns in England; of the cost of the system to this nation; of the forty-pounder Armstrong, adopted for the navy in 1859, and of the constructing of one hundred of the 110-pounders before any experiments with them had been concluded.

Of four guns under trial, three showed a separation on the outside between the trunnion-ring and the coil behind it. The fourth showed a separation all round, but to less extent. All the guns expanded in the shot chamber and part of the powder chamber, and the *bores were elongated.* Much of these defects, no doubt, arose from excessive friction between the lead-coated projectile and the gun, which caused an unnecessary stress upon the gun.

The first visit paid by the Board was to the Elswick works. They remark: "The establishment at Elswick is thoroughly equipped for heavy work, and has produced the largest guns in the world. . . . The shops are supplied with an abundance of fine tools," page 583. They have a hammer of thirty-five tons. "The advantages of the Whitworth manufacture are also recognised, and a forging press is being introduced."

They next visited the Woolwich Royal Gun Factories, which are stated to have had in 1873-4 a capacity for the production of 6,000 tons of guns of various calibres per year. "The transition state in which the Board found the Woolwich gun factories is due to the change from muzzle-loading to breech-loading, and the substitution of homogeneous metal for the wrought coil" (page 589). The Board give a list of the chief tools in the Arsenal, as boring machines, planing machines, &c. There are four travelling cranes of 60 tons, six of 30, and six of 25 tons capacity. There are also: one steam hammer of 40 tons, one of 12 tons, one of 10 tons, two of 7 tons, besides many smaller ones. The steam power in the Royal Gun Factories is supplied by forty boilers of 40-horse power. "The plant at Woolwich, because of its transition state, contains very little worthy of imitation in planning the erection of gun factories in the United States."

The Board next visited the works of T. Frith & Sons, Sir John Brown & Co., C. Cammell & Co., and Sir H. Bessemer, all of Sheffield, and Lieut. Jaques gives full accounts of the most recent furnaces and methods employed there in working steel, illustrated with many beautiful plates. He also gives an account of the manufacture of compound armour, under the patents of Wilson & Ellis; as well as of the trials of armour plate made at Spezzia, and of granite forts protected by iron plates at Shoeburyness in 1883.

"The new departure in the system of gun construction, described farther on in this report, will demand from the Sheffield steel manufacturers increased effort. Up to the present time the only portion in the construction of the Woolwich gun that required steel was the tube. . . . The new construction requires that steel shall be used throughout, and the castings for the jackets for guns now in hand at Woolwich can hardly be supplied from Sheffield" (page 630).

It is remarked that in one important establishment preparations were being made for the introduction of a large press, to take the place, or supplement, the work of the hammer. The Sheffield steel manufacturers are entirely sceptical as to the advantage or practicability of the compression of steel in the liquid state, and although they concede the efficacy of forging under hydraulic compression, they consider it an objection to the process that a much higher temperature will be required for the press than for the hammer.

Sir Joseph Whitworth's works at Manchester were

[1] *Proceedings* of the United States Naval Institute. vol. x. No. 4, 1884. (The Establishment of Steel Gun Factories in the United States, by Lieut. W. H. Jaques, U.S.N.)

plished in the year 1883, and that many of the lacunæ in our knowledge are being steadily filled in. The Molluscoidea seem to have had more than ordinary attention paid to them, and the record of this group by Prof. E. von Martin appears to be extremely well done. As usual, Messrs. W. H. Kirby and R. McLachlan record the enormous section of Insecta, the lion's share falling to the former, the latter confining his attention to the Neuroptera and Orthoptera. In his treatment of the general subject (Insecta) the recorder frequently quotes memoirs relating to the structure, &c., of the groups recorded by Mr. McLachlan, and it is not without interest to note that, while some of these are the subjects of a double record, others are not. One interesting fact, showing the importance which a "Zoological Record," when complete, is to the working naturalist, is alluded to by Mr. McLachlan in his remarks introducing us to H. de Saussure ("Mémoires pour servir à l'Histoire naturelle du Mxeque des Antilles, et des États-Unis. Orthoptères de l'Amérique moyenne: Famille des Blattides." Genève, 1864):—"This very important memoir is noticed at the request of the author. It escaped notice in the early volumes of this 'Record' (which commenced with the year 1864), and also in the German *Bericht*. It would also appear to have escaped the notice of workers on Blattidæ generally, for none of the new terms employed therein for generic, &c., division are included in Scudder's just-published laborious 'Universal Index' which extends down to 1879." Scudder's New Index is, however, far from being a full record of generic names in any one group.

The new names proposed for genera or sub-genera, as recorded in this volume, amount, the editor informs us, to 1079, as against 1015 of last volume, and this without including any of the Arachnidæ. Of these, no less than 115 require re-naming, having been already in use. This number affords no clue to the amount of new species described, which is considerably larger, thus indicating for the present no lack of work for the systematic zoologist.

The British Association for the Advancement of Science still continues its grant of 100*l*., and the Government Grant Committee of the Royal Society renewed its vote of 150*l*., while the Zoological Record Association itself keeps up both the number of its members and subscribers.

A Treatise on Practical Chemistry and Qualitative Inorganic Analysis. By Frank Clowes, D.Sc. Lond. Pp. xv., 376. Fourth Edition. (London: J. and A. Churchill, 1885.)

THIS well-known manual has reached a fourth edition. It very thoroughly fulfils the aim which is set forth in the preface, viz. to place trustworthy and practical methods of qualitative analysis in the hands of the student. If the chemical student must still devote a large amount of his time to qualitative testing, then he certainly could not do better than follow the directions of this book. But the very excellence of the tables and methods of the book before us makes us more than ever doubt the wisdom of attempting to teach the science of chemistry by a course of "test-tubing." The art can be learnt by rules and formulæ, but the science comes not by such as these.

This book only includes what "directly bears on the ordinary requirements of the laboratory student"; its directions are those of a man who knows what he is writing about, and who has learnt what he teaches by good honest work in the laboratory. It contains many of those results of laboratory experience which are usually preserved in the private note-books of the teacher, and which may almost be regarded as trade secrets. The only fault we have to find is that the book tends too much in the direction of recipes. Were a student to work conscientiously through the book he would certainly be an accomplished analyst, but we are afraid he might have ceased to be a chemist. However excellent rules and tables may be in their own way, it is possible to have too much of them. In fact, the better they are the less one wants to be bound by them. The "tables of differences" given in the book are excellent; in the hands of a good teacher they might be made the basis of a really scientific training. But the ordinary student will not trouble to develope methods from the facts set before him in these tables; he will pass on to the systematic examination of simple salts, and be caught in the fatal whirlpool of "experiment," "observation," "inference."

M. M. P. M.

Original Researches in Mineralogy and Chemistry. By J. Lawrence Smith. Edited by J. B. Marvin. (Louisville, 1884.)

IN a recent number (vol. xxxi. p. 220) we gave a statement of the life and work of the late Prof. J. Lawrence Smith condensed from a memoir prepared at the request of the National Academy of Sciences, Washington, by Prof. B. Silliman, who was so soon to follow his friend to his long rest. The papers containing the original investigations of Prof. L. Smith have now been collected together and reprinted as a memorial volume intended for presentation to his friends. Three memoirs prepared by Mr. Marvin, Mr. Michel, and Prof. Silliman respectively, form an appropriate introduction, and give one a good glimpse into his life and character. The work is clearly printed on good paper, and will be highly appreciated by his numerous friends, to each of whom a copy has been presented by his widow.

Lehrbuch der Mineralogie. Von Dr. Gustav Tschermak. Zweite, verbesserte Auflage. (Wien: Alfred Hölder, 1885.)

WE are glad to find that a second edition of this work is already called for, although the latter part of the first edition appeared so lately as 1884. In our notice of the first part of that edition (vol. xxiv. p. 355) we directed attention to the excellent character of the work, and gave a brief statement of its contents; we now need only remind our readers that the author is a thorough master of his subject, who has done a large amount of original and valuable work, and further, has had a long teaching experience as Professor of Mineralogy in the University of Vienna. The work is but slightly changed in the present edition; the length is increased by a few pages through the incorporation of the results of investigations made since the first part left the press in 1881; the contents are well up to date. If some University Professor would provide us with an equivalent work written in our own tongue the study of mineralogy in this country would begin to revive.

LETTERS TO THE EDITOR

[*The Editor does not hold himself responsible for opinions expressed by his correspondents. Neither can he undertake to return, or to correspond with the writers of, rejected manuscripts. No notice is taken of anonymous communications.*

[*The Editor urgently requests correspondents to keep their letters as short as possible. The pressure on his space is so great that it is impossible otherwise to insure the appearance even of communications containing interesting and novel facts.*]

Mr. Lowne on the Morphology of Insects' Eyes

I DESIRE to give an unqualified denial to the imputation made by Mr. Lowne in his letter to NATURE of April 9 (p. 528), that my opinion with regard to his paper on the structure of the eye in Arthropods was formed under the influence of my colleague, Prof. Lankester, or that any consultation upon the paper took place between us. References of papers for the Royal Society are strictly confidential, and I did not know the name of the second referee until after I had come to a conclusion upon the subject—a conclusion which was only arrived at as the result of a long and patient investigation of Mr. Lowne's preparations,

Prof Exner on Retinal Image in
Insect Eye

Mic Journal vol 1890 p 558

Nerve

"

"

Mr. Hickson [illegible] [illegible] [illegible]

[illegible] 12 [illegible] 1883

[illegible] [illegible] [illegible] [illegible]

[illegible] Carpenter on R[illegible] [illegible] Quart. Journal Oct 1885

Parietal Eye [illegible]

W. B. Spencer 13 May 1886

Eye Retina Quart. Micr. Journal

S. J. Hickson. Oct: 1880

" Limulus. Scorpion

Ray Lankester [illegible] [illegible]

" Chiton

H. N. Moseley Jan. 1885

" Insects

S. J. Hickson April 1885

Lower Retina Blind [illegible]

[illegible] [illegible] Journal

" [illegible] Feb [illegible]

H Virtue Tebbs -
With the writer's kind regards

[*Extracted from the* LINNEAN SOCIETY'S JOURNAL—ZOOLOGY, vol. xx.]

ON THE STRUCTURE OF THE RETINA OF THE BLOWFLY (*CALLIPHORA ERYTHROCEPHALA*).

BY

BENJAMIN THOMPSON LOWNE, F.R.C.S., F.L.S.,

HUNTERIAN PROFESSOR OF COMPARATIVE ANATOMY IN THE ROYAL COLLEGE OF SURGEONS.

On the Structure of the Retina of the Blowfly (*Calliphora erythrocephala*). By BENJAMIN THOMPSON LOWNE, F.R.C.S., F.L.S., Hunterian Professor of Comparative Anatomy in the Royal College of Surgeons.

[Read 21st February, 1889.]

(PLATE XXVII.)

IN 1884 I had the honour of reading a paper before this Society on the compound vision and morphology of the eye in insects, which was published in the second volume of the new series of 'Transactions.'

That paper received at the time much adverse criticism, and Dr. Hickson published a memoir in the 'Quarterly Journal of Microscopical Science,' in which he convinced himself that he had completely refuted my observations.

From that day to this I have continued to work at the subject, and I now venture to bring before this Society evidence which I think can hardly fail to convince even the most sceptical of my opponents. Although I never had any doubt of the correctness of my figures or descriptions, I felt it incumbent upon me to produce preparations which would admit of no double interpretation, but which would appeal at once to the eyes of those who are only partially acquainted with the histology of the vertebrate retina.

At the time I published my former paper I felt so certain that the views I held would receive a ready acceptance, that I did not, perhaps, enter sufficiently into minute details, and left many points to be investigated by other workers. I have since examined every structure in the greatest detail, and have much to add with regard to the developmental history of the compound eye.

The retinal rods, which I figured correctly in my former paper, correspond with the periopticon of Dr. Hickson, except that his figures show that every vestige of nerve-structure and nerve-terminal organs had been completely destroyed in his preparations, leaving nothing but the skeletal framework with the tracheal vessels, which he has delineated most carefully and correctly.

He states that my paper and investigations were unnecessary, owing to the unanimity of previous investigators: none, however, agree in any detail with Dr. Hickson, nor, so far as I am able to judge, to any considerable extent with each other.

Putting aside for the moment the earlier observers, the so-called periopticon of Hickson has only been described in detail by Berger, Carrière, Ciaccio, Viallanes, Hickson, and myself.

To show how far these observers agree with each other and with the older writers, I will quote a few sentences from Dr. Hickson's paper. He says:—

"Previous to the publication of Berger's paper the optic tract of insects had been briefly described and names given to the various regions. Thus Weismann called the opticon and epiopticon the 'bulbus,' the region where the optic fibrils decussate the 'Stiel,' and the periopticon the 'Augenscheibe'" (*l. c.* page 27).

Even the most cursory acquaintance with the work of the German naturalist would have shown Dr. Hickson that this is an egregious misstatement of Dr. Weismann's nomenclature.

Weismann's 'Stiel' was the optic nerve, and his 'Augenscheibe the structure from which the dioptron is developed. I shall have later to give Dr. Weismann's views more fully. Dr. Hickson continues (page 27):—"Since Berger's paper appeared Carrière has described the periopticon as 'a layer of long palisade-shaped cells, the number of which corresponds with the eye units; every one of these palisade cells possesses an oblong nucleus at its foremost, somewhat broader, end.' My researches show that this description is quite inaccurate. The elements of the periopticon are not cells, and the large oval nucleus situated in each element does not exist; nerve-cells, when they exist in the region of the periopticon in *Musca*, lie between the elements and not in them, as my figures show."

These statements and others show that Dr. Hickson and Carrière do not agree. With regard to the nuclei described by Carrière, they undoubtedly exist, but not, as Carrière thought, within the palisades, but externally to them, immediately beneath their investing sheath. Dr. Hickson is right when he says these bodies are not cells, they are developed from cells, and each consists of a bundle of fusiform rods. With regard to the terminations of the optic nerve, Carrière distinctly traced the nerve-fibres into the palisades; Dr. Hickson says they go round them. I trace them directly into the fusiform rods which form the palisades. The structure seen and correctly figured by Dr. Hickson are tracheal vessels.

Carrière supposed the nerve-fibres to pass out at the superficial end of the palisades and to perforate the basilar membrane; from this I entirely dissent. In support of this view Carrière has figured, quite diagrammatically, what I believe is a tracheal vessel seen behind the fusiform body. Carrière also saw the highly refractive outer ends of the rods, or, rather, that part which is connected with their inner portion, and says, "in *Musca vomitoria* one sees in every cell a cylindrical axis."

Dr. Hickson entirely put himself in the wrong in describing the nervous elements as between the palisades; his nervous elements are undoubtedly fine tracheal tubes. Dr. Hickson's figures accurately represent the nerve-sheaths and tracheæ as well as the supporting neuroglia, but no vestige of nerve or nerve-end organs appears in them. A careful examination of his own figures at once leads to a dissent from all his statements, which are as inaccurate as his figures are accurate. I cannot understand how so good an observer could have been so misled.

Berger and Viallanes trace the optic-nerve fibres through a series of small round cells, very conspicuous in the outer half of my retina, Hickson's periopticon. Hickson regards these cells as of quite secondary import. They clearly belong to the supporting tissue and are external to the sheaths of the retinal elements, which are continuous with the perineurium of the optic nerve.

Dr. Hickson and Dr. Grenacher suppose the sheathing cells of the great rods, retinulæ of Grenacher, to be the nerve-terminals; and more recently Platten pretends that the optic nerve terminates in the crystalline cone. There is therefore no unanimity amongst previous writers, especially in matters of detail; as it is impossible that they can all be right, it is quite possible, as I assert, that they are all wrong.

Dr. Hickson's neurospongium, or terminal anastomosis, which is inadmissible on physiological grounds, is no nerve-plexus at all, but the tracheal plexus and the sustentacular framework of my retina.

It is exceedingly difficult to prepare sections which show the true retinal end-organs. This difficulty arises from the fact that the chloroform and alcohol used in the process of imbedding dissolve the fatty matters from the nerves, and the external extremities of my retinal rods are completely dissolved or disintegrated by the action of aqueous media.

I have, however, on many occasions succeeded in obtaining sections in which both the inner and outer extremities of the retinal rods, as well as the nerves, remain more or less unaltered. Another difficulty arises from the extreme transparency of these structures in very thin sections, and from the fact that they cannot be stained by any of the stains used in such researches; the outer ends of the rods are not affected by strong solutions of aniline dyes, except vesuvin *.

In thicker sections the numerous round cells between the retinal nerve-end organs, which are not connected with nerves, but with the sustentacular framework, entirely conceal the outer ends of the rods.

There are two methods which give good results; in both the tissues must be fixed either with osmic acid and absolute alcohol

* The best demonstration of these organs is obtained by staining with a solution of vesuvin in aniline water. The solution must be quite freshly made, and unfortunately such preparations fade rapidly when mounted in balsam.

or in absolute alcohol, and imbedded in paraffin without the use of ether or turpentine. Very thin sections are then cut and fixed on the slide with shellac and kreosote. The cement must be thoroughly dried in the oven at the melting-point of the paraffin used, and on no account at a higher temperature.

The paraffin is next removed by turpentine. The slide is then wiped on its back and edges, and flooded with pure spirit, which is drained off, and immediately afterwards flooded with 75 per cent. alcohol and rapidly drained; Erhlich's logwood solution is then poured on the slide and washed off after a few minutes or longer by agitating the slide for a few moments in water, and it is again flooded with 75 per cent. alcohol. The washing is the most dangerous process, as if the specimens are kept too long in water the outer ends of the retinal rods will be entirely dissolved. Instead of Erhlich's logwood a solution of vesuvin in water may be used; it stains the retinal-end organs better than any of the aniline dyes. Saffranine in 50 per cent. alcohol, or a solution of fuchsine or eosine, may be used for staining, and the washings done with spirit, the results of which are often satisfactory. Spiller's purple gives excellent results, but the specimens are not permanent. The specimen, after flooding with 75 per cent. alcohol, is treated with pure alcohol, rapidly drained and cleared with clove-oil and mounted in balsam.

Or, after the first washing in water, the specimen may be mounted in glycerine, gradually adding stronger and stronger glycerine and water, and draining after each addition. I have found that with aniline dyes a very dilute solution of sodium carbonate, ·5 per cent., or aniline water is not inadmissible for washing out the excess of the stain.

Glycerine mounts, when successful, show the outer ends of the rods, either vacuolated or frequently partially dissolved, more plainly than balsam mounts.

The balsam mounts need very careful illumination, otherwise it is impossible to see the outer ends of the rods.

If we trace the optic nerve, we observe that its fibres run in larger or smaller bundles, invested in a very transparent sheath, or perineurium. They terminate in the palisade layer by entering the fusiform elements. The sheath is continued over the fusiform elements, and terminates on the inner surface of the basilar membrane. The tracheal vessels accompany the bundles of optic nerve-fibres, outside their sheath, and continue between the pali-

sades, and ultimately pierce the basilar membrane and run between the great rods.

The figure given (Plate XXVII. fig. 1) is from the eye of a Hawk-moth, in which these details are larger and more easily seen than in the Blowfly. The palisade bodies do not reach the basilar membrane, but are prolonged as extremely transparent rods, 3 to 5 μ in diameter, in the fly and in most of the insects I have examined, and from 20 to 30 μ in length (Plate XXVII. figs. 2 and 3, *a*). These with the palisade cells, *b*, form my bacilli or retinal end-organs, the whole length of which is from 60 to 70 μ. The outer transparent portion is rarely straight, but usually strongly curved in a crook. They exhibit a fine longitudinal striation.

The outer ends of the rods evidently consist of some substance resembling mucin; they have the same refractive index and general characters as the mucin of the intestinal epithelial cells of the insect.

The inner extremity of the outer part of the rod is imbedded in the fasciculus of elongate cell-like palisade bodies, fig. 2, which form the inner portion of the retinal end-organs; each outer segment appears to be made up of a number of finer rods, 2 μ in diameter, pressed together into a cylinder; these produce the longitudinal striæ. Each small component rod lies on the inner surface of one of the fusiform cell-like bodies which form together the inner part of the retinal end-organ.

The outer ends of the rods are surrounded and, except in very thin sections, concealed by the small round chaplet-cells of Viallanes (fig. 2, *c*). These are connected with each other by fine processes and form a true adenoid sustentacular tissue, well seen in transverse sections of the pupa (fig. 4).

Comparison of the Bacillary Layer with the Bacillary Layer of the Vertebrate Retina.

In size and structure the elements of the retina are almost identical with those of the vertebrate; the optic nerve terminates in the protoplasmic inner segment, whilst the outer segment is transparent, resists stains, exhibits longitudinal striæ, and swells up with water in both. In both it is easily destroyed, and frequently exhibits vacuolation.

In most insects the outer, highly refractive ends of the retinal end-organs are imbedded in abundant pigment. The flies are the only exception, and in these the cells surrounding the bacilli are free from pigment.

The Tracheæ (Plate XXVII. fig. 3) form a dense network around the inner segments of the retinal end-organs in insects, and branches extend to and perforate the basilar membrane. These fine tracheæ are without any spiral markings, and are easily mistaken for fine nerve-twigs. The figure given (fig. 3) shows these tracheæ in a moth, and it can be readily seen that they lie between the nerve-end organs, and that they branch dichotomously between the great rods. The aniline stains at once colour the tracheæ, whilst they have no effect upon the nerves. These stains, however, attack the nerve-sheaths, but not the outer ends of the retinal end-organs. By the use of aniline stains, especially Spiller's purple, I have been able to trace the finer tracheal vessels, which have been constantly mistaken for nerves, to the larger tracheal trunks and in one of my photographs this relation is sufficiently evident.

The illustrations on Plate XXVII. show the large size of the bundles of optic nerve-fibres with their terminations in the retinal end-organs; they also show that nothing bearing any proportion to the magnitude of these nerve-cords passes through or even up to the basilar membrane. The basilar membrane is chitinous and has a cellular layer on both its inner and outer surface; that on its inner surface consists of branching or stellate cells, which are continuous with the sustentacular framework of my retina; the outer layer consists of pigment-cells, continuous with the pigment-sheaths of the great rods. The perforations in the chitinous layer of the basilar membrane are between and not opposite to the extremities of the great rods, and transmit the tracheal vessels.

The structure of the great rods has with some been the difficulty in accepting my views. The appearance of these structures in many sections is certainly perplexing. The reason is that which I have already insisted upon. In life they are hollow tubes filled and distended with fluid. In bad preparations they appear stellate in transverse sections and present no central cavity; in radial sections they are separated from each other by wide spaces, often filled by distended tracheal vessels.

In transverse sections, when unaltered by the process of imbedding, they are circular or hexagonal rings, with a large central cavity; they touch each other at their periphery, and the tracheal vessels appear as thick-walled but very small tubes. Each great rod is seen in such sections to be lined by a thin cuticular layer, which dips down between the sheathing cells; it is the folds of this membrane which appear as bright highly refracting points under unfavorable conditions of illumination. With direct central light, thin sections, with oil or water immersion-lenses, no longer present these appearances; there is no bundle of axial rods in such preparations when properly examined, only a thin cuticular lining.

Further evidence in favour of my views is, I believe, shortly forthcoming from the pen of an independent observer. Prof. Plateau informs me that last year, at Cologne, Dr. Exner showed the single image formed by the compound eye—the image in the plane of my basilar membrane formed by the uninjured eye, *i. e.* by my dioptron. I wait anxiously for the spring, as with fresh insects at command I have little doubt the demonstration of an erect picture in this region is perfectly easy.

The Development of the Compound Eye.

The development of the compound eye was described by Weismann in 1864 *. I have gone through a most laborious research, and in the main points my observations agree with those of the great German investigator. Weismann says it has long been known that the eye in insects is developed from two perfectly distinct parts—one from the nerve-centres of the larva, the other from the optic disc ("Augenscheibe," *l. c.* p. 194).

If we follow the development of the optic disc, we find it at first as a thin cellular expansion enveloping the anterior part of the hemisphere (or supra-œsophageal ganglion). It consists of cells (the optogenic cells of Viallanes) which are larger than those of the other discs; they measure 15 μ in diameter at an early period of the pupa state and have large clear nuclei. During the formation of the head, the eye-disc separates considerably

* "Die Entwicklung der Dipteren," Leipzig, 1864. Reprinted from Köll. Zeitsch. f. w. Zool.

from the hemisphere, the interspace being filled with the granular yelk-like substance of the somatic cavity of the pupa. The whole dioptron is developed by a division of the optogenic cells, as Claparède long ago showed. Each original cell corresponds to a single corneal facet. These cells form almost hemispherical projections on the outer surface of the disc and are soon covered by an extremely thin cuticular layer.

The cuticular layer is seen in my sections to dip slightly between the cells, whilst the corneal lens is secreted subsequently between the cell and the primitive cuticular layer. The lenses are, as I have already described them, perfectly distinct from the chitinous layer, giving rise to the condition I have designated the kistoid cornea. In adult pupæ the distinction is perfectly apparent, although Dr. Hickson has denied that my description is correct; the most patient reinvestigation entirely confirms my former statement.

So far my investigations entirely accord with Weismann's description. Weismann, however, believes that the great rods contain a nervous structure, which he describes, from optical sections, as resembling a bundle of fine, highly refractive, conducting threads ending at the crystalline cone. He has nothing to say of their manner of development, and only expresses the opinion that they appear more like definite threads than the angles of a solid rod.

These so-called axial threads, as I have stated above, are well seen in numerous transverse sections to be mere folds of a chitinous membrane enclosing a considerable empty cavity.

Weismann's description of the development of the nervous structures is as follows:—"The thin nerve-cord (*Stiel*) which unites the optic disc to the hemisphere still appears on the fifth day as a nervous cord; but on the twelfth day the pedicle can no longer be seen." He concludes, however, that it has spread out into an invisible layer over the whole surface of the ganglion. That he should have arrived at such a conclusion without sufficient evidence is quite unlike him. If, as he says and as is certainly the case, the nerve disappears entirely between the fifth and twelfth day, the opinion that the radial striæ (which, he says, appear later between the disc and the hemisphere) are the same nerve spread out, is not founded on fact.

We must remember that Weismann regarded the discs as

expansions consisting of epiblast-cells. It was Ganin who, ten years later, first made sections and discovered their real structure. He found three distinct layers—Weismann's epiblastic layer; his own provisional layer, which covers it externally as a fine cellular expansion, which resembles the amnion of a mammalian embryo in being continuous with the periphery of the disc, in covering its whole outer surface, and in enclosing a cavity between it and the epiblast of the disc; and the mesoblastic layer, which fills the hollow cup-like cavity on the inner surface of the epiblastic layer, and which consists of a network of fine branching cells.

Weismann's own figure (52, plate xiii., *l. c.*) shows clearly that his supposed optic nerve is the mesoblast of the disc. My own observations show that the nervous pedicle of the optic disc becomes atrophied and disappears, whilst the nervous retina is developed as a papilla in front of the original optic pedicle.

In my former paper I described and gave figures of the manner in which a new retina is developed during the skin-shedding of the Cockroach; the original nervous pedicle of the disc corresponds to the nerve of the first few facets of the eye. As the number of facets is far greater after each ecdysis, so a new retina is developed from the nerve-centres as a distinct papilla; the first formed nerve and retina at the same time undergo atrophy.

I regard the original pedicle of the disc in the Blowfly (figs. 5, 6, & 7, *st.*) as a rudiment. It exhibits few, if any, nerve-fibres and consists chiefly of connective neuroglia continuous with the investing layer of the rudimentary hemisphere. The spongy mesoblastic tissue which Weismann mistook for an expansion of the nervous pedicle of the disc consists of the elements from which the tracheal vessels and pigmented fringes of the dioptron and neuron originate. This tissue extends into the dioptron, but only between the ingrowing optogenic cells, which become first columnar and then elongated rods, dividing during the process to form the cone and the investing cells of the great rods, and separating from each other to enclose the central cavity of the cone and the great rod. Claparède long ago correctly described the manner of the development of the cones and great rods.

Viallanes, like Weismann, but with less excuse, mistook the mesoblast of the disc for the optic nerve and believed that its fibres perforate the axes of the great rods. It is easy in thick

sections to mistake fibres running between for fibres entering the optogenic cells.

The nerve-papilla, from which the optic ganglia, the optic nerve, and the retina are developed, gradually grows outwards towards the dioptron (Plate XXVII. figs. 5–8, *n*). It is at first covered by a layer of columnar cells, which represent the epiblast of the nerve-centre; from this layer the bacillary layer of the retina is developed. These cells become converted into the retinal end-organs. The mesoblastic spongy tissue is gradually absorbed or converted into tracheal and connective elements, which ultimately form a thin layer between the retina and the basilar membrane of the dioptron.

The retina, even when the insect is nearly ready to escape from the pupa, is still separated from the dioptron by a space filled with branching cells (Plate XXVII. fig. 8, *mc*) and secondary yelk, so that the supposed entrance of nerve-fibres into the dioptron cannot be explained by any known process of development.

The continuity of the tracheæ of the dioptron and those of the mesoblast is the result of the penetration of the latter between the great rods during their inward growth; but during this period the nervous papilla is separated by a wide space filled with secondary yelk and reticular mesoblast from the ingrowing epithelial structures of the dioptron.

Thus, if my observations are correct, the retina, like that of a vertebrate, is entirely formed as an outgrowth from the central nervous system, while the dioptron, like the crystalline lens and the refractive structures generally, is formed from the external epiblast, which is more or less invaded by mesoblastic elements. With regard to the retina itself, it is undoubtedly, like the nerve-centres, no less epiblastic in the insect than in the vertebrate, as the hemispheres themselves, as well as the ventral ganglia, are formed from the embryonic epiblast.

In conclusion, I would add that it is scarcely fair to expect me to prove a negative, *i.e.* that no nerve-fibres pass to the dioptron. The onus rather lies with my opponents to prove that the great optic nerve does enter the dioptron, and to find its terminals. Even the most cursory glance at the works of Dr. Hickson, M. Berger, M. Viallanes, and others will show that they have given totally dissimilar representations; of these Dr. Hickson's are correct enough as representations of tracheal and mesoblastic skeletal tissues. I would ask, Which of the various structures

represented are to be considered as nerves? No one has yet figured one satisfactory representation of the optic-nerve fibres entering the great rods. Dr. Hickson says, "Morphology teaches us that the great rods are nerve-terminals." To appeal to morphology to settle the question appears to me to show on how slender a basis of observation the received view rests, and I should myself regard an appeal to morphology as one which is fatal to the received view; for, if morphology teaches us anything on this subject, it is that the retinal end-organs belong to that part of the epiblast from which the great nerve-centres are developed, and that the dioptric structures arise from the superficial or cutaneous epiblast.

DESCRIPTION OF PLATE XXVII.

Fig. 1. A section of the retina of a Hawk-moth; partly drawn from a photograph and finished from the section. *gt*, great rods; *m*, basilar membrane; *b*, bacillary layer; *n*, optic nerve; *tr*, tracheal vessel.

2. A section of the retina of a Blowfly. *c*, chaplet-cells of Viallanes. $\frac{1}{12}$-inch objective, water-immersion.

3. A portion of the retina of a Hawk-moth; drawn from a photograph, with details added from the specimen. The tracheal vessels seen passing through the basilar membrane are much more distinct in the photograph than in the specimen seen by the microscope; these are represented in the drawing as they appear in the photograph.

4. A transverse section through the bacillary layer of the retina of a Blowfly which had just emerged from the pupa.

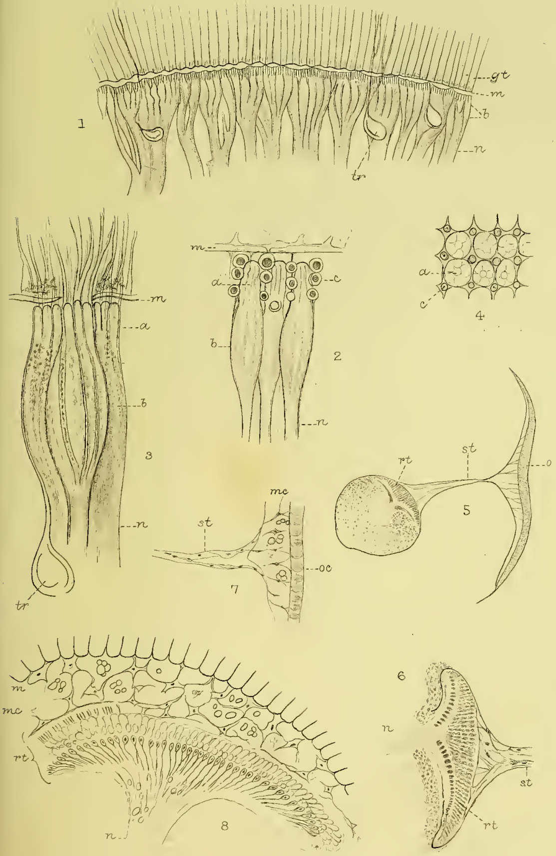
5. A section of the optic disc and cephalic ganglion of a 3-day-old pupa. *o*, optic disc; *st*, stalk; *rt*, retina. 1-inch objective.

6. A portion of the same, showing the retina and inner extremity of the stalk.

7. A portion of the optic disc and stalk of the same. *oc*, optogenic cells; *mc*, mesoblastic cells. $\frac{1}{4}$-inch objective.

8. A section of the retina of a ten-day-old pupa. Showing the mesoblast elements between the retina and the basilar membrane. $\frac{1}{4}$-inch objective.

(The letters indicate the same parts in all the figures.)



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RETINA OF BLOWFLY.